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REVISION OF *HILLIA*  
(RUBIACEAE)<sup>1</sup>

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ABSTRACT

*Hillia* Jacq. is a genus of 24 usually epiphytic species that are distinguished by their convolute corolla aestivation and comose seeds. Based on corolla characters, five subgenera are recognized here: subgenus *Hillia* (six species), subgenus *Andinae* C. M. Taylor (one species), subgenus *Tetrandrae* C. M. Taylor (five species), subgenus *Illustres* C. M. Taylor (seven species), and subgenus *Ravnina* (Oersted) C. M. Taylor (five species). Keys to all species of the genus are provided, and those of the first four subgenera are described and illustrated.

*Hillia* Jacq. is a genus of 24 species of usually epiphytic shrubs distributed widely in the moist and wet Neotropics. These species are easily separated from all other Rubiaceae by their seeds with a tuft of "trichomes" 1–3 cm long attached at one end, and can usually also be recognized by a succulent epiphytic habit, caducous ligulate stipules that are interpetiolarly connate, solitary flowers, and cylindrical woody capsules. The corollas may have one of several combinations of color and form: white and salverform, green to yellow-green or red and funnellform, or red and tubular to inflated.

Species of *Hillia* can be confused with those of *Cosmibuena* Ruiz & Pav., which are succulent

epiphytes with a similar geographic range, similar capsules, and salverform white corollas similar to those of some species of *Hillia* (Taylor, 1992). *Cosmibuena* can be distinguished by its glabrous seeds, interpetiolarly and partially intrapetiolarly connate stipules, and usually three or more flowers per inflorescence. Steyermark (1974) also distinguished *Hillia* by the lack of marginal wings on the seeds; however, many seeds of *Hillia* have at least a thin marginal wing, while the seeds of *Cosmibuena* are variable in this regard. These genera can usually also be separated by their stigmas, which are bilobed, densely papillose, and held above the anthers in *Cosmibuena*, in contrast to subcap-

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itate to bilobed or linear, less densely papillose, and sometimes held below the anthers in *Hillia*. Other characters used to separate these genera by previous authors were discussed by Taylor (1992).

*Hillia* was published with the single species *H. parasitica* Jacq., the most widespread and common species in the genus, which he described from the Antilles. The name commemorates Sir John Hill (1716–1775), a “pompous” (Smith, 1814) British apothecary and “author of several voluminous but useless botanical works” (Sims, 1804), and it has been suggested that the specific epithet was intended as much to describe Hill’s botanical work as the plant’s habit. *Hillia* has not been treated comprehensively since de Candolle (1830) recognized three species. Reviews of its characteristics, relationships, and notable species were presented by Bentham & Hooker (1873), Schumann (1889, 1891), and Steyermark (1963, 1972). Descriptions of individual species or local groups of species may be found in various regional treatments covering areas from southern Mexico and the Antilles through Peru, Bolivia, and southern Brazil.

*Saldanha* Vell. was first combined with *Hillia* by Schumann (1889), who included species with both salverform white corollas and funnelform green corollas in this genus. However, the variation in corolla form encompassed within the genus has not been recognized by all authors, particularly those working in Central America where representatives of subgenus *Illustres* C. M. Taylor were unknown until recently. Based on a survey of this variation, the Central American genus *Ravnia* Oerst. was recently reduced to a subgenus of *Hillia* (Taylor, 1989). In spite of the considerable variation in corolla form, subgenus *Ravnia* (Oerst.) C. M. Taylor was the first subgenus published in *Hillia*. In the present treatment I recognize five subgenera: subgenus *Hillia* (six species), subgenus *Andinae* C. M. Taylor (one species), subgenus *Tetrandrae* C. M. Taylor (five species), subgenus *Illustres* (seven species), and subgenus *Ravnia* (five species).

Species of subgenus *Hillia* are found through most of the range of the genus, with the exception of Central America and Mexico. *Hillia parasitica* is found throughout the range of this subgenus; the remaining species are found from northern to central South America. In contrast, species of subgenus *Tetrandrae* are primarily found in the Greater Antilles and Central America, with one extending southward along the northwestern coast of South America. Species of subgenus *Illustres* are found in South America, with one extending north to Costa Rica. Several species of subgenus *Illustres*

show wide geographical disjunctions, suggesting that they are uncommon or that the epiphytic flora of this region is poorly collected. Species of subgenus *Ravnia* are found in southern Central America, with two recently described species extending the range of this subgenus to southern Mexico and Venezuela (Taylor, 1991).

#### MORPHOLOGY

The morphology of subgenus *Ravnia* has been described previously (Taylor, 1989). The discussion presented here applies to the species of *Hillia* including those of subgenus *Ravnia*.

#### HABIT, STEMS, AND VESTITURE

Plants of *Hillia* are erect or sometimes clambering succulent shrubs, small trees, or lianas; habit is variable in most species. They are usually epiphytes but may also be terrestrial or rheophytic (*H. rivalis* C. M. Taylor). *Hillia parasitica* is frequently rooted in soil, although in Puerto Rico this species is found rooted only on wet mountaintops where the soil is saturated throughout the year (Ewel & Whitmore, 1972) and root growth of most plants is limited. The branches of most species are elongate, to a meter or more in length, and flexuous. The stems may be quadrate when young, but usually become rounded with age. The bark is usually smooth and grayish brown, but may be deep reddish brown in occasional individuals of some species. Such reddened bark appears to be correlated with reddened stipules and corollas that are flushed with pink in individual plants. The bark of *H. killipii* Standley has a distinctive coppery red color and thin papery texture, and is usually wrinkled or circumferentially ridged, particularly on young twigs. Plants of all species are glabrous throughout. Raphides are found in all parts, but are particularly evident in the stipules, ovaries, and abaxial surface of the leaf veins.

#### LEAVES

The leaves are isophyllous (or anisophyllous in some plants of *Hillia triflora* (Oerst.) C. M. Taylor) and petiolate (or subsessile in *H. costanensis* Steyermark.), although the blades may be attenuate at the base and the petiole difficult to delimit precisely. The blades are succulent, entire, and generally elliptic to oblanceolate or lanceolate. The secondary veins are pinnate with at least one pair of veins arising distally to the middle of the blade, or subpalmate in *H. ulei* K. Schum. and *H. oaxacana* C. M. Taylor, with all of the veins arising proximally

to the middle of the blade. The veins are usually plane, or the secondary veins may be prominulous to prominent abaxially in some species of subgenus *Hillia*, and the higher order venation is characteristically prominulous as well in *H. bonoi* Steyererm. In most species the venation is indistinct due to the succulence of the leaves. Domatia are generally lacking, although occasional crypt or pocket domatia are found in *H. bonoi* and *H. macrophylla* Standl.

The stipules are interpetiolar, ligulate to oblanceolate, and caducous. They are finely veined in a subparallel, subpalmate pattern. They become pale green to white before falling, or red in some individuals of some species. The flowering nodes are usually subtended by stipules that are similar in shape and size to those of vegetative nodes; these stipules are also usually caducous, but in some individuals of some species they persist until anthesis. Such persistent stipules have been called "bracts" by some authors (e.g., Steyermark, 1972, 1974). These structures are here called "stipules subtending flowers."

#### FLOWERS

The flowers are terminal and solitary, infrequently three in *H. illustris* K. Schum. and *H. saldanhae* K. Schum., or usually three in *H. triflora*. They may be sessile or borne on stout peduncles and sometimes also short pedicels. Bracts are rare and resemble the stipules in shape and texture, but are much smaller. These bracts have been called "bracteoles" by some authors (e.g., Steyermark, 1972, 1974). The flowers are homostylous and apparently protrandrous. The duration of a single flower is unknown.

The calyx limb may be completely divided into four to six lobes, or as many as nine or ten in some species of subgenus *Illustres*; have a well-developed tube and short lobes, as in *Hillia costanensis*; or be completely absent in some individuals of some species, apparently never forming in the flower bud. This last condition may be what Schumann (1891) described as "caducous." The calyx limb typically persists until anthesis and often remains on the fruit. Size and shape of the calyx lobes frequently vary widely within a species.

The corollas may be salverform with relatively long slender tubes (subg. *Hillia*, subg. *Andinae*, subg. *Tetrandrae*), narrowly to broadly funnelform (subg. *Illustres*, subg. *Ravnia*), or tubular to inflated (subg. *Ravnia*). The salverform corollas have slender tubes and spreading lobes, and are white or sometimes flushed with pink or red in individuals

of some species. They are strongly and sweetly fragrant at night, and are most likely pollinated by hawkmoths or other nocturnal vectors. The funnelform corollas have tightly reflexed lobes and are green sometimes flushed with yellow, pink, orange, dull purple, salmon, or bright red. Nothing is known about their odor or pollination, but they seem to be adapted for bat pollination. The tubular and inflated corollas also have tightly reflexed lobes and are red and odorless and apparently pollinated by birds. The corollas are membranaceous to thickly carnose; those of all species are glabrous throughout. There are usually four to six lobes, to as many as nine or ten in some species of subgenus *Illustres*. The number of lobes frequently varies within a species. Aestivation is contorted with the lobes oriented to the right, the less common condition in the Rubiaceae than leftward orientation (Robbrecht, 1988).

The stamens are inserted near the mouth of the corolla tube, or near the middle of the tube in subgenus *Tetrandrae*, subgenus *Andinae*, and some species of subgenus *Illustres*. They are usually equal in number to the corolla lobes, although they may be more or fewer in individuals of species of subgenus *Illustres*. The filaments are usually short, and the anthers are usually included. The anthers are bithecal and dehiscent by longitudinal slits, with the filaments attached near their bases. The pollen is reportedly 3-colporate (Robbrecht, 1988) or 3-porate (Andersson & Persson, 1991).

The style is straight and slender and is surrounded at the base by a low annular disk. The two stigmas are subcapitate or linear-elongate and usually positioned at or just above the anthers, or in subgenus *Tetrandrae* and subgenus *Andinae* in the lower part of the corolla tube below the anthers. The style is glabrous; the stigmas are usually papillose.

The inferior ovary is turbinate to cylindrical, with axile placentas that bear numerous ascendingly imbricated ovules. The ovary is sometimes narrowed to stipitate at the base.

#### FRUITS

The mature capsules are cylindrical, pale green to brown, woody, and smooth, or longitudinally ridged. Dehiscence is septicidal and basipetal, with the valves then opening longitudinally along the middle of the septum. The old valves often remain attached to the plant after the seeds are dispersed, with the fibrous exocarp and mesocarp separating from the papery endocarp. The capsules of most species terminate in a beak 1–10 mm long that is

composed of the enlarged and hardened disk and sometimes also an apical extension of the ovary above the attachment of the calyx limb. The capsules are stipitate in most species of subgenus *Illustres* and also in subgenus *Andinae* and *H. rivalis*. In some individuals the stipe is not evident on the flower, but elongates markedly during fruit development.

The narrowly rhombic seeds are strongly flattened with a small elliptic to rhombic embryo 1–3 mm long, and are partially edged by a thin membranaceous to papery margin or wing. A tuft of straight brown trichome-like processes or filaments about 1–3 cm long is attached to the acroscopic end. These processes have been regarded as outgrowths of the seed wall rather than “true” trichomes (Robbrecht, 1988). They apparently aid in wind dispersal, both by providing a sail and by attracting animals: hummingbirds pry open capsules of *Hillia parasitica* in Puerto Rico and remove seeds for nest construction, releasing numerous other seeds to the wind in the process (pers. obs.).

#### CLADISTIC ANALYSIS

The classification presented here and for *Cosmibuena* (Taylor, 1992) is based on cladistic analyses of the individual species of *Hillia* and *Cosmibuena*, along with representatives of several genera of Cinchoneae. These analyses were directed at (1) the relationship among the epiphytic neotropical genera *Hillia*, *Cosmibuena*, and *Balmea* Martínez; (2) the relationship of *Hillia* to the Cinchoneae; (3) the relationships among the species of *Cosmibuena*; and (4) the relationships among the species of *Hillia*.

#### INGROUPS

The taxa analyzed were the four species of *Cosmibuena* recognized by Taylor (1992), *Balmea stormae* Martínez of northern Mesoamerica, and the twenty-four species of *Hillia* recognized in the present treatment.

#### OUTGROUPS

Four neotropical genera often classified in the Cinchoneae (Robbrecht, 1988; Andersson & Persson, 1991) were chosen as outgroups. These genera were chosen based on features shared with one or both genera of interest: *Ladenbergia* Klotzsch includes several species that are similar to *Cosmibuena* in stipule, inflorescence, floral, fruit, and seed morphology; *Ferdinandusa* Pohl species have inflorescence and corolla morphology similar to that

of *Cosmibuena* and capsules similar to those of all three epiphytic genera; *Cinchona* L. has salverform corollas and capsules similar to those of all three epiphytic genera, though with acropetal dehiscence; and *Coutarea* Aubl. has funnellform white to pink corollas with five to six reflexed lobes and convolute or imbricate aestivation, and woody capsules with marginally winged seeds. The removal of *Coutarea* from the Cinchoneae to the Condamineae has recently been proposed (Andersson & Persson, 1991); this genus is included in the present analysis based on the similarity of its corollas to some species of *Hillia*.

Two neotropical genera classified in other tribes, *Rondeletia* L. (Rondeletieae) and *Arcytophyllum* Roem. & Schult. (Hedyotideae), were chosen as outgroups based on their clear affinities outside of the Cinchoneae (Robbrecht, 1988), their capsular fruit, and their relatively recent morphological and systematic review. *Rondeletia* is here regarded in the wide sense as accepted by Lorence (1991); its morphology has also been summarized by Borhidi (1982), Kirkbride (1968), and Steyermark (1967). Characteristics of *Arcytophyllum* are based on the treatment by Mena (1990).

#### CHARACTERS

This analysis is based on morphological characters. The characters used and their states are shown in Table 1. Several of these (#1, 4, 5, 11, 26) are autapomorphies and were excluded in some analyses. The character states coded for each species are shown in Table 2.

Because examination of the relationships among the epiphytic groups was one of the goals of this analysis, habit was not included as a character. Quantitative characters were partitioned so that the number of polymorphic taxa was minimized. Polymorphic taxa were coded for the condition that was presumably less derived, based on outgroup comparison.

#### ANALYSIS

Several groups of analyses were made, using both PAUP (Swofford, 1990) and Hennig86 (Farris, 1988):

1. considering all species and using all of the characters listed in Tables 1 and 2, analyzed heuristically, with the characters treated variously as ordered or unordered;
2. considering all species and excluding the autapomorphic characters, analyzed heuristically, with the characters treated variously as ordered or unordered; and

TABLE 1. Characters and character states used in cladistic analyses. Characters denoted with an asterisk (\*) are autapomorphic in individual species and were eliminated in some analyses; see text for further explanation.

1	dry color of plants*: 0 = green, 1 = reddish brown.
2	raphides: 0 = absent, 1 = present.
3	pubescence: 0 = plants with trichomes on vegetative portions, 1 = plants glabrous throughout.
4	bark texture*: 0 = smooth, 1 = wrinkled.
5	bark color*: 0 = brown, 1 = coppery red.
6	leaf size: 0 = more than 12 cm long, 1 = 6-12 cm long, 2 = 0.5-5 cm long.
7	leaf apex: 0 = acute to acuminate, 1 = rounded.
8	leaf texture: 0 = chartaceous, 1 = subcoriaceous, 2 = coriaceous.
9	leaf venation prominence: 0 = all prominent abaxially, 1 = primary and secondary veins prominent abaxially, 2 = primary vein prominent abaxially.
10	leaf venation pattern: 0 = pinnate, 1 = subpalmate.
11	number of secondary veins: 0 = 9-10 pairs, 1 = 3-8 pairs.
12	anisophylly*: 0 = absent, 1 = present.
13	stipule connation: 0 = interpetiolar, 1 = interpetiolar and intrapetiolar.
14	number of flowers: 0 = 3 to many, 1 = 1-3, 2 = 1.
15	corolla shape: 0 = salverform, 1 = funnellform, 2 = tubular, 3 = inflated.
16	corolla color: 0 = white, 1 = green, or green flushed with yellow or orange, 2 = green flushed with red, 3 = salmon red, 4 = bright red.
17	corolla aestivation: 0 = convolute, 1 = imbricate, 2 = valvate.
18	corolla lobe number: 0 = 4, 1 = 5-7, 2 = 8-10.
19	corolla lobe length: 0 = 8-15 mm, 1 = 16-25 mm, 2 = more than 25 mm.
20	corolla tube internal epidermis: 0 = glabrous, 1 = papillose.
21	calyx limb form: 0 = tube present, 1 = absent or divided to base.
22	anther position: 0 = included to slightly exserted, 1 = exserted.
23	stigma shape: 0 = subcapitate, 1 = with two linear branches, 2 = with two divergent, strongly flattened branches.
24	stigma position: 0 = below anthers, 1 = above anthers, included, 2 = above anthers, exserted.
25	stipe on capsule: 0 = absent, 1 = present.
26	capsule texture: 0 = papyraceous, 1 = woody.
27	capsule surface*: 0 = smooth to slightly longitudinally ridged, 1 = longitudinally winged.
28	capsule dehiscence: 0 = basipetal, 1 = acropetal.
29	comose seeds: 0 = absent, 1 = present.

TABLE 2. Character state coding used in the cladistic analyses. The characters and their states are numbered as defined in Table 1. "?" indicates missing data. Taxon abbreviations are as follows: ROND *Rondeletia* (Rondeletieae); ARCY *Arcytophyllum* (Hedyotideae); LADE *Ladenbergia* (Cinchoneae); FERD *Ferdinandusa* (Cinchoneae); COUT *Coutarea* (Cinchoneae or Condamineae); CINC *Cinchona* (Cinchoneae); BALM *Balmea*; CGRA *Cosmibuena grandiflora*; CMAC *Cosmibuena macrocarpa*; CMAT *Cosmibuena matudae*; CVAL *Cosmibuena valerii*; HBON *Hillia bonoi*; HKIL *H. killipii*; HMAB *H. macbridei*; HMAM *H. macromeris*; HMAP *H. macrophylla*; HPAR *H. parasitica*; HWUR *H. wurdackii*; HPAN *H. panamensis*; HLOR *H. loranthoides*; HMAX *H. maxonii*; HPAL *H. palmana*; HTET *H. tetrandra*; HCOS *H. costanensis*; HFOL *H. foldatsii*; HGRA *H. grayumii*; HILL *H. illustris*; HPSA *H. psammophila*; HSAL *H. saldanhae*; HULE *H. ulei*; HALL *H. allenii*; HLON *H. longifilamentosa*; HPIT *H. triflora* var. *pitieri*; HOAX *H. oaxacana*; HRIV *H. rivalis*; HTRI *H. triflora* var. *triflora*.

	Characters						
	12345	67891	11111	11112	22222	2222	
	0	12345	67890	12345	6789		
ROND	00000	00000	00002	01000	00110	0000	
ARCY	01000	20220	10002	02000	00110	0000	
LADE	00000	00100	00000	02101	00210	1000	
FERD	00000	00000	00000	00110	00010	1000	
COUT	00000	10000	00001	00110	01010	1000	
CINC	00000	00000	00000	02110	00210	0010	
BALM	01100	10100	10002	40100	10110	1000	
CGRA	01100	00120	10100	01111	00210	1000	
CMAC	01100	00120	10100	01111	00210	1000	
CMAT	01100	11220	10100	01111	00210	1000	
CVAL	11100	11220	10120	00111	10210	1000	
HBON	01100	00200	00020	00110	10010	??0?	
HKIL	01111	10010	10020	00120	10010	1001	
HMAB	01100	20220	10020	00110	10101	1001	
HMAM	01100	00010	10020	00120	10010	??0?	
HMAP	01100	00210	10020	00120	10010	1001	
HPAR	01100	10120	10020	00120	10010	1001	
HWUR	01100	10010	10020	00110	10010	??0?	
HPAN	01100	21120	10020	00000	10100	1001	
HLOR	01100	10220	10020	00010	10100	1001	
HMAX	01100	11220	10020	00010	10100	1001	
HPAL	01100	21220	10020	00000	10100	1001	
HTET	01100	11120	10020	00010	10100	1101	
HCOS	01100	10220	10021	10100	00021	1001	
HFOL	01100	11220	10021	20100	10021	1001	
HGRA	01100	00220	10021	10100	10010	1001	
HILL	01100	00220	10011	10100	10021	1001	
HPSA	01100	10220	10021	10100	10011	??0?	
HSAL	01100	11120	10011	?0100	10011	??0?	
HULE	01100	00221	10021	10200	10011	1001	
HALL	01100	10220	10021	30100	10020	1001	
HLON	01100	10220	10021	30110	11020	1001	
HPIT	01100	10220	11013	40100	10020	1001	
HOAX	01100	10221	10021	20100	10020	1?0?	
HRIV	01100	10220	10021	20100	10021	1001	
HTRI	01100	10220	10012	40100	10020	1001	

3. considering subsets of species and excluding the autapomorphic characters, analyzed heuristically and with complete algorithms, with the characters treated variously as ordered or unordered.

Each subset of species included several outgroups, at least one member of each of the genera and subgenera under analysis, and all of the species of a particular focus group. *Cosmibuena* and each subgenus of *Hillia* were taken in turn as focus groups.

Autapomorphic characters were eliminated from the second and third sets of analyses because they were uninformative with regard to relationships among species. Subsets of species were used in the third group of analyses because the large number of species included in the full analyses, 36 in all, exceeds the size at which either cladistic analysis package is predicted to return a good response (Swofford, 1990). Only heuristic procedures could practically be employed with the full data set (first and second groups of analyses); one exhaustive search was attempted using Hennig86, but was unsuccessful and terminated after more than nine days of run time.

**Results.** Identical cladograms were obtained using both PAUP and Hennig86. Selected cladistic hypotheses will be presented and evaluated below; their systematic implications will be discussed in subsequent sections on classification and relationships. It should be clear from the hypotheses presented below that the morphological data available do not unequivocally indicate a single probable phylogenetic relationship among these species. However, these data do generally support the classification system proposed here; more detailed work is left to future systematists.

The first group of analyses found five equally most parsimonious cladograms. One of these is shown in Figure 1. In all of these cladograms, *Balmea* was grouped with *Hillia* subg. *Ravnica*; *Hillia*-*Balmea* was monophyletic; *Cosmibuena* was arranged as a grade immediately basal to *Hillia*; *Hillia*-*Balmea*-*Cosmibuena* was monophyletic; and *Hillia* subg. *Tetrandrae* was monophyletic. The strict consensus of these five cladograms is shown in Figure 2. These five cladograms differed in the arrangement of the species of subgenus *Hillia*, which were variously arranged as a clade or grade; in the relationships among the species of subgenus *Illustres*, which were arranged as a grade in all cladograms; and in the relationships of species of subgenus *Illustres* with those of subgenus *Ravnica*.

The second group of analyses found three equally most parsimonious cladograms. One of these is shown in Figure 3. The strict consensus cladogram obtained from these analyses is shown in Figure 4. In all of these cladograms, *Cosmibuena* was ar-

ranged as a monophyletic group placed within *Hillia*; *Hillia*-*Cosmibuena* was monophyletic; *Balmea* was placed immediately basal to this group; *Hillia*-*Cosmibuena*-*Balmea* was monophyletic; and subgenus *Tetrandrae* was monophyletic. The cladograms differed in the arrangement of species of subgenus *Hillia*, which were always arranged as a grade; in the arrangement of the species of subgenus *Illustres*, which were always arranged as a grade; and in the relationships of the species of subgenus *Illustres* with those of subgenus *Ravnica*.

Results from the third group of analyses are not presented here. These did not contradict previous analyses and added no information.

#### TRIBAL CLASSIFICATION OF *HILLIA*

The position of *Hillia* within the Rubiaceae has been the subject of significant disagreement, and its placement has been altered as ideas about the systematics of the family have evolved.

Schumann (1891) agreed with earlier authors in placing *Hillia* in the Cinchoneae DC., distinguished by capsular fruit with ascendingly imbricated winged seeds, of the subfamily Cinchonoideae Raf., distinguished by numerous ovules in each locule.

Verdcourt (1958) proposed the next, extensively revised classification of the Rubiaceae, utilizing new characters and assumptions. Verdcourt placed *Hillia* in his subfamily Rubioideae, which was distinguished by the presence of raphides. *Hillia* occupied an isolated position within this subfamily and was not classified further, although Verdcourt suggested that it might be placed in its own monotypic tribe.

Bremekamp (1966) reviewed the Rubiaceae in further detail, drawing on his own and Verdcourt's work and basing his classification on various characteristics including sculpturing of the testa walls and the presence or absence of raphides, which he considered to have evolved only once in the family. Bremekamp placed *Hillia* in subfamily Hillioideae Bremek. ex S. P. Darwin along with *Ravnica* Oerst. and *Deppea* Schltld. & Cham., based on the presence in all three genera of raphides, contorted corolla aestivation, and a distinctive exotestal cell structure that was otherwise found only in *Gleasonia* Standl. *Deppea* has since been shown to have little relationship to *Hillia* and has been placed in its own tribe (Kirkbride, 1982) or more recently in the Hamelieae DC. (Bremer, 1987). *Ravnica* has been synonymized with *Hillia* (Taylor, 1989), and thus *Hillia* occupies an isolated position in Bremekamp's classification.

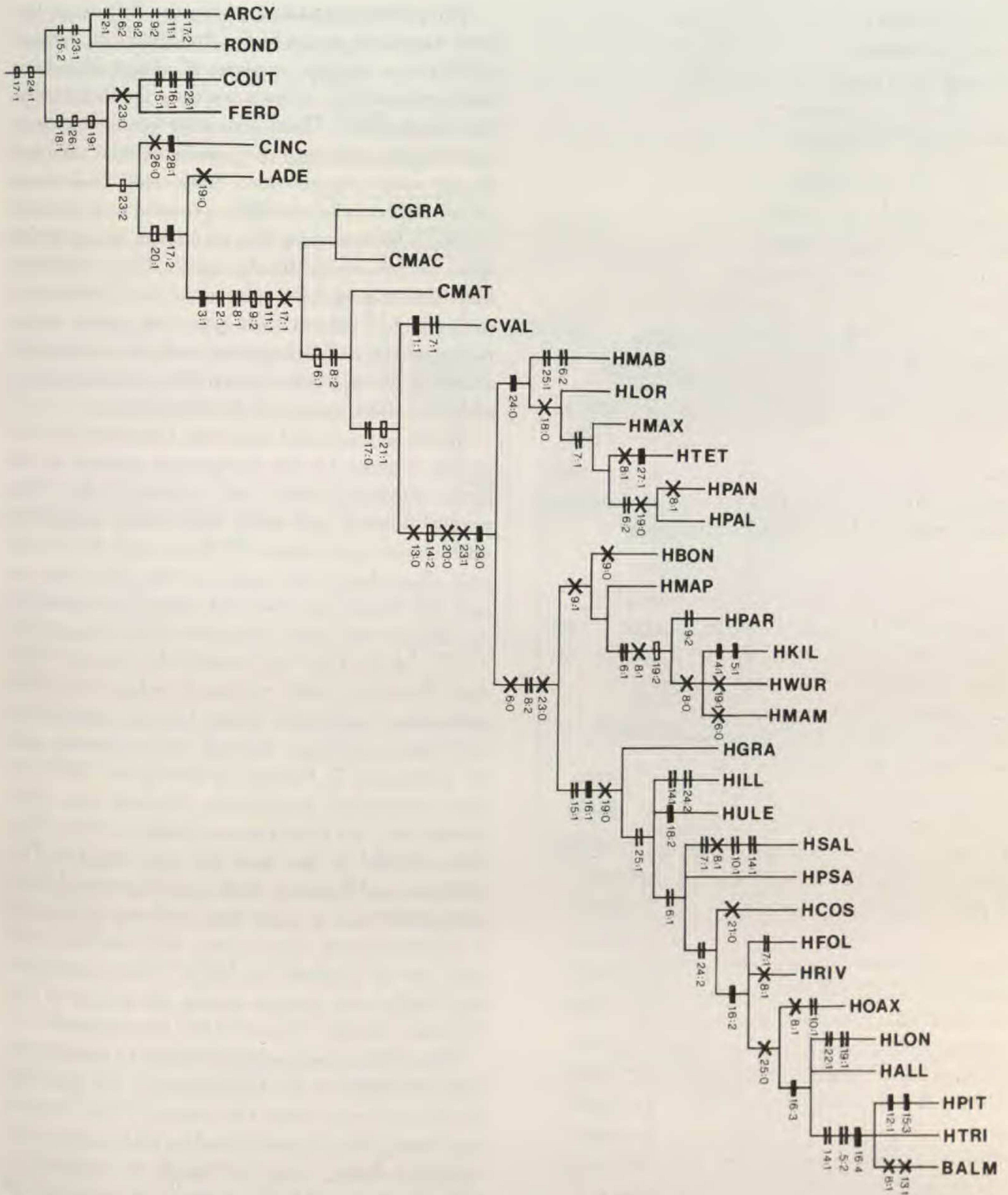


FIGURE 1. One of five most parsimonious putative phylogenies of *Hillia* and *Cosmibuena* species obtained from the first set of analyses as described in the text, based on the full character set presented in Table 2. Analysis was heuristic (Hennig86: mhennig\* and branch-breaking options); characters were treated as ordered; polarity was determined by majority rule among outgroups. Numbers designating characters and their states are defined in Table 1; four-letter codes designating taxa are defined in Table 2. Black rectangles indicate synapomorphies that are not reversed on the cladogram; open rectangles indicate synapomorphies with reversals on the cladogram; crosses indicate reversals; parallel lines indicate parallelisms. See also discussion in the text and Figure 2.

The most recent comprehensive classification of the Rubiaceae was proposed by Robbrecht (1988). Raphides probably have arisen repeatedly in the Rubiaceae (Robbrecht, 1988), and he again placed *Hillia* in the Cinchonoideae. Robbrecht indicated

that within this subfamily *Hillia* is related to the Cinchoneae but "reduced," in fact "an extreme case of this trend." He maintained *Hillia* in its own tribe, citing "many characters justifying its separation as a monogeneric tribe," but without

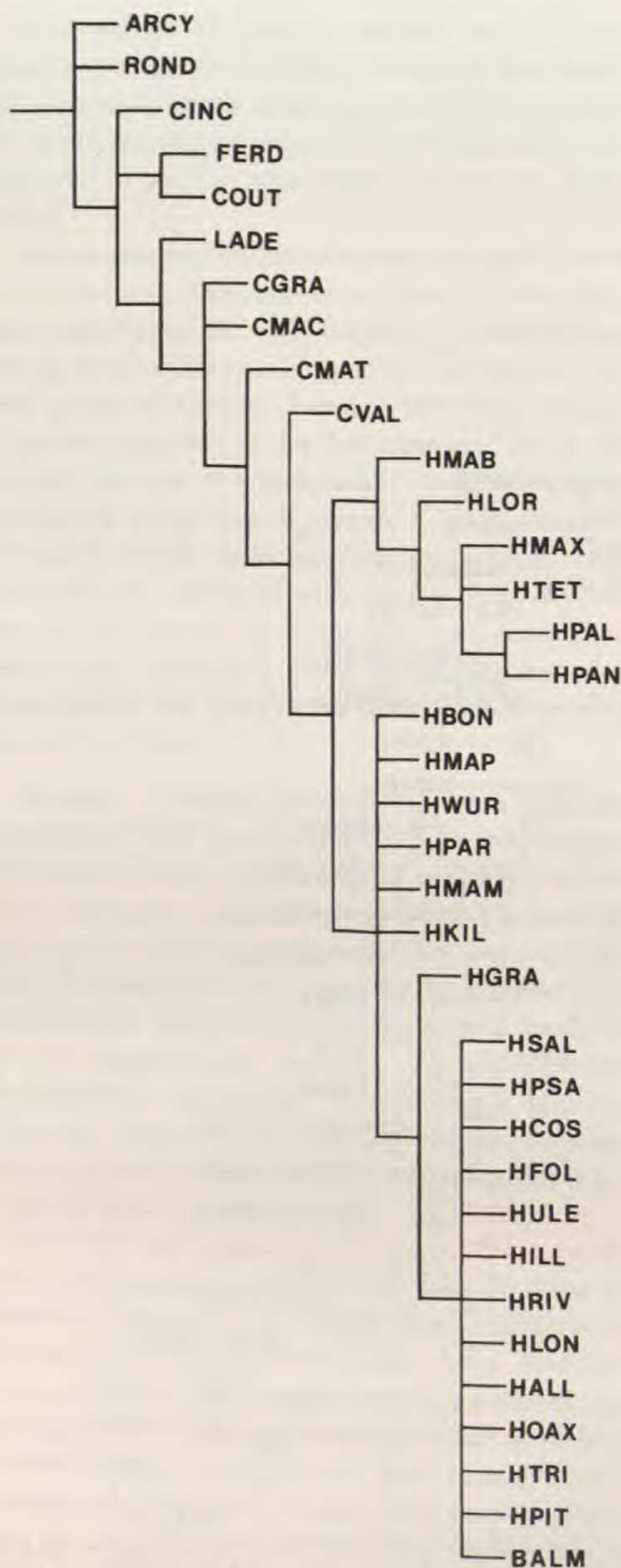


FIGURE 2. Strict consensus tree of the five cladograms obtained in the first set of analyses described in the text. Four-letter codes designating taxa are defined in Table 2.

listing them. This classification apparently depends heavily on the comose seeds. Robbrecht concluded that these structures are better regarded as outgrowths or extensions of the testa wall, and thus homologous to the testa walls of other species rather than trichomes. However, he did not otherwise explain the difference between these epidermal outgrowths and other epidermal outgrowths classified as trichomes.

The position of *Hillia* within the Rubiaceae has been examined in detail by Andersson & Persson (1991) in a cladistic analysis of genera that have been proposed by various authors for inclusion in the Cinchoneae. Their character set is extensive and reliable, although the results of their analyses do not seem unequivocal. Andersson & Persson found *Hillia* to be variously grouped as a member of their Cinchoneae s. str., as a sister group of this tribe, or as a more distant taxon. They concluded that *Hillia* is closely related to the Cinchoneae, with which it shares fruit type and similar sculpturing of the radial exotestal wall, but maintained *Hillia* in its own tribe, which they considered possibly the sister group of the Cinchoneae.

*Hillia* is separated from the Cinchoneae s. str. in this scheme by the sculpturing pattern of the inner tangential testa wall; solitary rather than several flowers; and seeds with scanty endosperm and comose appendages. Of these, only the comose seed appendages are unique in the entire data set and the Rubiaceae. Several other characteristics are shared with some members of the Cinchoneae s. str., where they are considered derived: wood rays 4-seriate; pollen porate or colporate; corolla aestivation contorted; pollen tectum imperforate; and habit epiphytic. Several characteristics used by Andersson & Persson to distinguish *Hillia* are here considered inaccurate, although this information may not have been available to them: calyx lobes divided to the base are also found in *Cosmibuena* and *Balmea*, while many species of *Hillia* completely lack a calyx limb and one species has a well-developed calyx tube; and fusiform seeds may not be confined to *Hillia* if the variation in seed shape and margin among all species of Cinchoneae, notably *Cosmibuena*, is considered.

Thus *Hillia* seems closely related to genera presently classified in the Cinchoneae s. str. and may be derived from within this group. *Hillia* seems to represent a line characterized by adaptations to an epiphytic habit, many of which are unusual or uniquely derived. Most of these features are not found in the Cinchoneae and therefore are used to exclude *Hillia* from that group, but the characters on which this decision is based do not seem conclusive. Homoplasious characters, as the exotestal wall sculpturing and raphides appear to be (cf. Bremekamp, 1966), are poor indicators of relationship, while autapomorphic features such as the comose seeds do not indicate any relationship.

Classification of *Hillia* therefore seems to depend on character weighting: this genus can be isolated in a monotypic tribe based on its uniquely derived features, or it can be included as a relatively derived member of the Cinchoneae, based on the



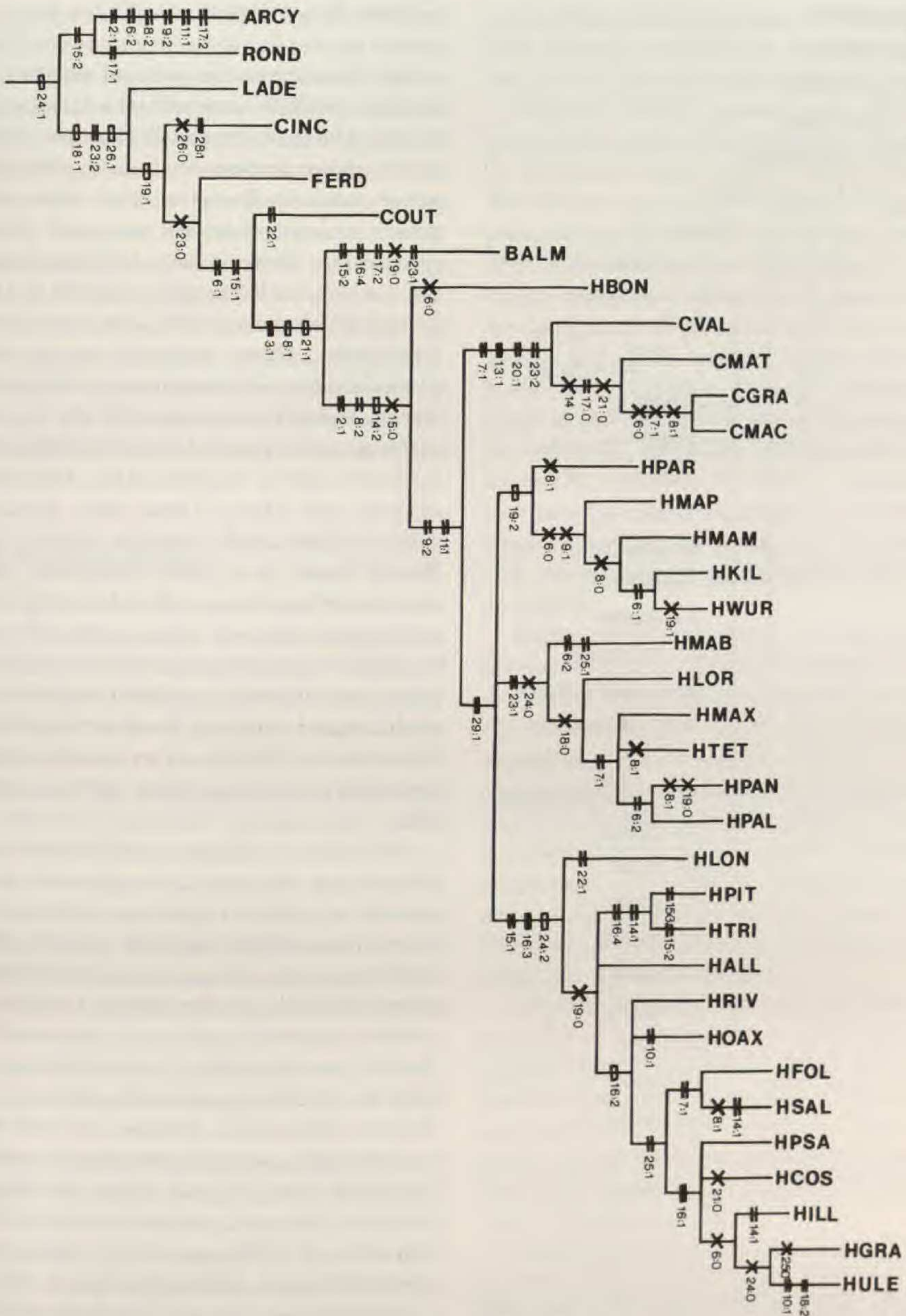


FIGURE 3. One of three most parsimonious putative phylogenies of *Hillia* and *Cosmibuena* species obtained from the second set of analyses as described in the text, based on a subset of the characters presented in Table 2, excluding autapomorphic characters. Analysis was heuristic (Hennig86: mhennig\* and branch-breaking options); characters were treated as unordered; polarity was determined by regarding *Ladenbergia* as ancestral. Numbers designating characters and their states are defined in Table 1; four-letter codes designating taxa are defined in Table 2. Symbols are the same as in Figure 1. See also Figure 4 and discussion in the text.

characteristics it shares with that group. Isolating *Hillia* in a monotypic tribe requires the assumption that the characteristics that distinguish it are all derived independently from the character states seen in the Cinchoneae, rather than as part of a transformation series. However, the comose seeds

of *Hillia* and the narrowly shaped, strongly erose seed margins of *Cosmibuena*, terminating in sparse filaments that resemble the numerous filaments of *Hillia*, need not have arisen independently, but may be steps in a transformation series. If the characters are viewed in this way, isolating *Hillia*

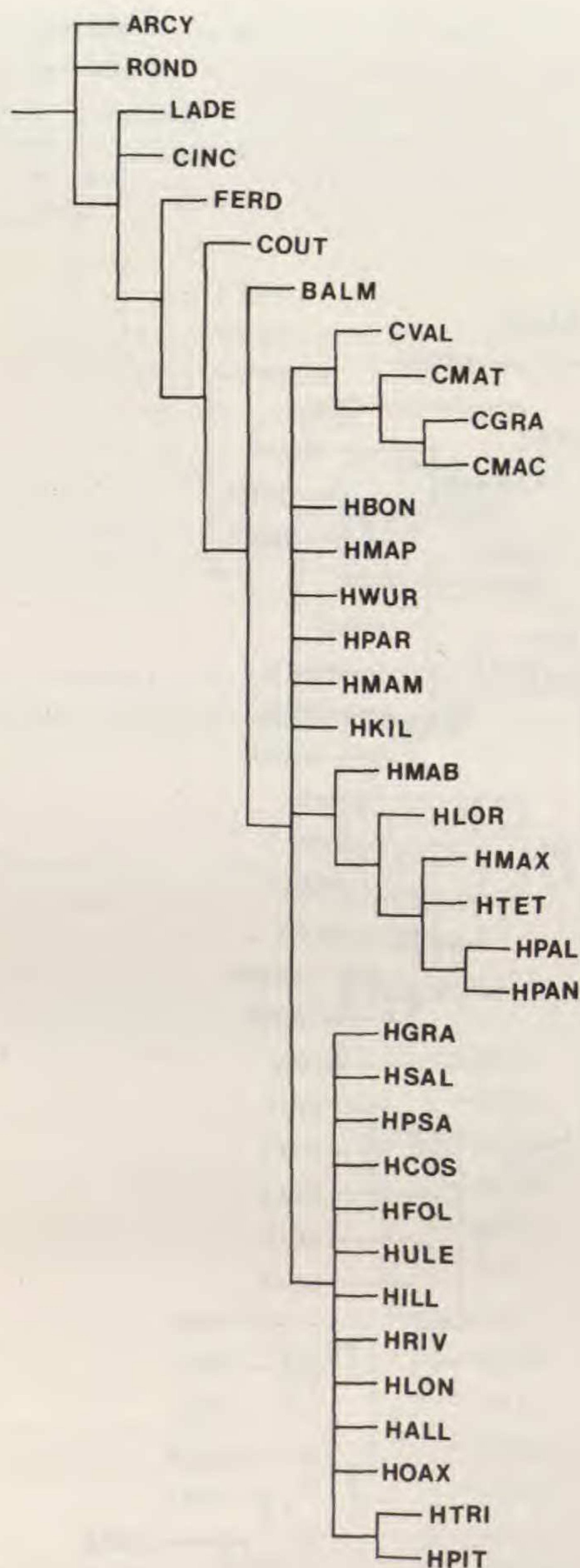


FIGURE 4. Strict consensus tree of the three cladograms obtained in the second set of analyses described in the text. Four-letter codes designating taxa are defined in Table 2.

results in an arbitrary separation of the derived end of an evolutionary trend toward reduction, in order to emphasize its distinctness rather than its relationships. Classification seems more useful when it reflects relationships rather than emphasizes distinctness, and *Hillia* is here considered a member of the Cinchoneae, probably closely allied with *Balmea* and *Cosmibuena*.

#### GENERIC RELATIONSHIPS OF *HILLIA*

As discussed in the previous section, the relationships of *Hillia* are with the Cinchoneae (Robbrecht, 1988; Andersson & Persson, 1991). Most of the characteristics that distinguish *Hillia* are either unique or found in many other rubiaceous genera and are therefore not good indicators of relationship. However one, epiphytic habit, is unusual within the Rubiaceae yet found in a few other genera (Robbrecht, 1988), and thus is potentially informative. Other epiphytic genera sometimes placed in the Cinchoneae are *Balmea*, *Cosmibuena*, and *Hymenodictyon* Wall.

*Hymenodictyon* includes about 20 occasionally epiphytic species found in Asia, Indonesia, Madagascar, and Africa. These differ markedly from *Hillia* in their small triangular stipules; numerous flowers borne in a dense, bracteate, spicate or capitate inflorescence; reduced funnelform to campanulate corollas with valvate aestivation; fusiform to elliptic stigmas that function as a pollen presentation mechanism; loculicidal capsules; lack of raphides; and vestiture of well-developed trichomes (Verdcourt, 1988). Based on these characters, *Hymenodictyon* does not seem closely related to *Hillia*.

*Balmea* is a monotypic genus found in southern Mexico and adjacent Guatemala that shares with species of *Hillia* a glabrous, rather succulent, sometimes epiphytic habit; the presence of raphides (Andersson, pers. comm.); a calyx limb almost completely divided into five lobes; a tubular to funnelform dark red corolla with five convolute lobes that are strongly reflexed; shortly linear styles; and beaked, cylindrical, septicidally dehiscent capsules. *Balmea* differs from *Hillia* in its small triangular stipules; eight or more flowers borne in pedunculate branched cymes; capsule valves that are partially divided at the apex; and seeds that are not comose (Standley & Williams, 1975). *Balmea* may be closely related to *Hillia* (cf. Figs. 1-4).

*Cosmibuena* is a genus of four species found from southern Mexico to Peru that share with *Hillia* a glabrous, succulent, usually epiphytic habit; the presence of raphides; large ligulate to oblanceolate stipules; three to several flowers borne in a terminal cyme or fascicle; salverform white corollas; porate pollen (Andersson & Persson, 1991); and beaked, cylindrical, septicidal capsules. *Cosmibuena* differs from *Hillia* in its intrapetio-larly fused stipules; usually shortly tubular calyx limb (completely divided in *C. valerii* (Standl.) C. M. Taylor); quincuncial corolla aestivation; bilobed

densely papillose stigmas; sculpturing of the inner tangential testa wall; and seeds that are not comose (Taylor, 1992). *Cosmibuena* seems closely related to *Hillia* and also to *Balmea*. Cladistic analysis indicates several possible relationships among these three epiphytic genera, from polyphyly (Andersson & Persson, 1991) to forming a monophyletic group (Figs. 1–4). The presence of raphides in *Cosmibuena* has been overlooked by some authors (e.g., Bremekamp, 1966; Robbrecht, 1988): the segregation of these genera has been based in part on this one feature and deserves reexamination. However, *Cosmibuena* also shares some features with *Ladenbergia* and other genera of Cinchoneae that are not found in *Hillia*, so the systematics of this group are far from resolved.

#### INFRAGENERIC SYSTEMATICS

Five subgenera are recognized here, three newly described. The delimitation of these subgenera is based primarily on the shape, number of lobes, and color of the corolla. The corolla features are generally correlated with similarities in stigma form and position relative to the anthers and the top of the corolla tube. The stigma and corolla characters may be shared in unrelated species with similar pollination syndromes, but stigma condition in conjunction with corolla form appears to be useful for phylogenetic inference in the Rubiaceae (Bremer & Jansen, 1990). The geographic coherence of the resulting subgenera and the presence of additional features shared by members of each group support the classification proposed here.

Subgenus *Tetrandrae* is the most clearly delimited of these groups. It is distinguished by its white salverform corollas with four lobes. These flowers are fragrant at night and are presumably pollinated by sphingids or other types of moths. White salverform corollas probably represent the ancestral condition in the genus and are also found in subgenus *Hillia* and subgenus *Andinae*. The four-lobed condition is otherwise unknown in *Hillia* and apparently represents a reduction from the five- to ten-lobed corollas that characterize the other subgenera. The species of subgenus *Tetrandrae* additionally share relatively short styles and linear stigmas positioned below the middle of the corolla tube and far below the anthers, which are situated at the mouth of the tube. This stigma morphology and position are otherwise found only in *H. macbridei* Standl. of subgenus *Andinae*, which differs in its five-lobed corolla. Within subgenus *Tetrandrae* most species have rounded leaf apices and

corolla lobes. Several species of this subgenus also have relatively small leaves and flowers, although they are not the only such reduced taxa.

Subgenus *Hillia* appears to be the basalmost group in the genus. This subgenus is characterized by salverform white corollas with five to six lobes. The flowers are strongly fragrant at night and are presumably pollinated by sphingids or other moths. The bilobed stigmas are subcapitate to somewhat elongated and positioned above the anthers. Several species have leaf domatia and well-marked secondary leaf veins, and the higher-order venation is also well marked in *H. bonoi* Steyerl. A wide range of leaf and flower sizes is represented within this subgenus, including the largest flowers in the genus (*H. macromeris* Standl.). Subgenus *Hillia* may be a diverse basal assemblage of species rather than a monophyletic group; the characters available are insufficient to distinguish between these possibilities.

*Hillia macbridei* appears to be intermediate between subgenus *Hillia* and subgenus *Tetrandrae* in its floral morphology: it shares the characteristic stigma position and morphology of subgenus *Tetrandrae*, while its corollas with five to six long narrow lobes are characteristic of subgenus *Hillia*. Vegetatively this species is unique in its reduced lanceolate leaves that are acute and usually stiffly coriaceous. All cladistic analyses consistently grouped this species as the sister group of subgenus *Tetrandrae*. This species is here placed in its own subgenus, subgenus *Andinae*.

Subgenus *Illustres* and subgenus *Ravnina* share funnellform corollas with five to ten lobes and subcapitate stigmas positioned at or just above the anthers. This stigma morphology is also shared with some species of subgenus *Hillia*. These two subgenera appear to be more closely related to each other than to the other subgenera of *Hillia*, and relatively more derived.

Subgenus *Illustres* is characterized by corollas that are predominantly green, although they may be flushed with yellow, orange, pink, or red. Nothing is known of the floral biology of these species, but the flowers appear to be adapted for pollination by bats. With the exception of *H. grayumii* C. M. Taylor, the species of this section are also characterized by stipitate fruit. Subgenus *Illustres* includes the widest variation in leaf form, anther position, and number of corolla lobes, although there appear to be no patterns or trends in this variation. Subgenus *Illustres* (excluding subg. *Ravnina*) may represent a grade rather than a monophyletic group; the morphological characters avail-

able are insufficient to distinguish between these possibilities.

Subgenus *Ravnia* is characterized by red corollas with six to seven lobes. The odorless flowers are presumably pollinated by birds and thus diurnal. This group was discussed in detail by Taylor (1989). Two species have been added subsequently to that treatment (Taylor, 1991), expanding the geographic range of the subgenus but not altering its characteristics. This subgenus is apparently the most derived.

The separation of subgenus *Ravnia* from subgenus *Illustres* is based exclusively on flower color and presumed pollination syndrome. Given the similarity between the two floral morphologies, red diurnally pollinated flowers could have arisen more than once. Subgenus *Ravnia* is here assumed to represent a monophyletic group, but further study may show that some of its species are better classified in subgenus *Illustres*.

#### TAXONOMIC TREATMENT

This study is based on study of herbarium specimens from the institutions listed in the acknowledgments, supplemented by fieldwork in Puerto Rico, Hispaniola, Dominica, Costa Rica, and Colombia. Measurements of soft parts given here are based on dried specimens; plants of *Hillia* are fleshy, and shrinkage of about 8–10% in soft parts accompanies the preparation of herbarium specimens.

**Hillia** Jacquin, Enum. Syst. Pl. 3. 1760. TYPE: *Hillia parasitica* Jacq.

*Fereiria* Vell. ex Vand., Fl. Lusit. Bras. Spec. 21, t. 1, fig. 8. 1788. TYPE: *Fereiria vellozoana* Schult. & Schult. f., Syst. Veg. 7: 83. 1829. [= *Hillia parasitica* Jacq.]

*Saldanha* Vell., Fl. Flum. 141. 1825. TYPE: *Saldanha nobilis* Vell. [= *Hillia parasitica* Jacq.], lectotype designated here.

*Ravnia* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjoebenhavn 1852: 49. 1853. TYPE: *Ravnia triflora* Oerst. [= *Hillia triflora* (Oerst.) C. M. Taylor.]

Shrubs, small trees, suffrutescent herbs, or lianas, slightly to strongly succulent, epiphytic or sometimes terrestrial or rarely rheophytic (*H. rivalis*), erect or sometimes clambering, glabrous throughout, with raphides; stems quadrate, usually becoming terete; bark smooth or rarely papyraceous and wrinkled circumferentially to peeling (*H. killipii*), gray to brown or sometimes red-brown or rarely coppery red (*H. killipii*). Leaves opposite,

decussate, isophyllous or rarely anisophyllous (*H. triflora* var. *pittieri*), petiolate or rarely sessile (*H. costanensis*); blades elliptic to very narrowly elliptic or ovate, entire, fleshy, drying membranaceous to coriaceous, rarely with pocket or crypt domatia (*H. bonoi*, *H. macrophylla*); secondary veins pinnate or rarely subpalmate (*H. oaxacana*, *H. ulei*), ascending, distal veins usually looping to interconnect, margins flat or rarely revolute (*H. bonoi*, *H. macbridei*, *H. rivalis*); stipules interpetiolar, caducous or those subtending flowers sometimes persisting until anthesis, ligulate to oblanceolate, membranaceous to subcoriaceous, with fine subparallel subpalmate venation, becoming pale green to white or sometimes reddened just before falling. Flowers terminal, solitary or rarely 2–3 in a sessile cyme (*H. illustris*, *H. saldanhae*, *H. triflora*), homostylous, apparently protandrous, with peduncles and pedicels stout, sometimes subtended by bracts, these similar to stipules but reduced in size; calyx with limb deeply divided or sometimes lacking or rarely with a well-developed tube and short lobes (*H. costanensis*), green, with lobes 4–10, sometimes variable in number within a species or an individual plant; corollas salverform (subg. *Hillia*, subg. *Andinae*, subg. *Tetrandrae*) to funnelform (subg. *Illustres*, subg. *Ravnia*), tubular (subg. *Illustres*, subg. *Ravnia*), or swollen (*H. triflora*), white (subg. *Hillia*, subg. *Andinae*, subg. *Tetrandrae*) to green sometimes flushed with yellow, pink, orange, or dull purple (subg. *Illustres*), or salmon to bright red (subg. *Ravnia*), with lobes 4 (subg. *Tetrandrae*) to 10, when more than 6 then sometimes variable in number within a species or individual plant, aestivation contorted to right; stamens usually equal in number to corolla lobes, inserted near top or middle of corolla tube, the filaments flattened to winged, very short to lacking or elongated, the anthers narrowly oblong to ellipsoid, bithecal, dehiscent by longitudinal slits, attached near base, partially to fully included or rarely exserted (*H. longifilamentosa*); ovary inferior, bilocular, turbinate to cylindrical, sometimes stipitate, the ovules numerous, vertically imbricate, borne on axile placentas; disk annular; styles straight; stigmas 2, subcapitate to shortly or elongated-linear, papillose, positioned at or just above or sometimes well below anthers. Fruit capsular, cylindrical, woody, smooth or sometimes longitudinally ridged to rarely winged (*H. tetrandra*), usually with beak formed by old disk and sometimes also the elongated ovary apex, septocidally and basipetally dehiscent; seeds flattened, elliptic to rhombic, with membranaceous to papyraceous

marginal wings, with tufted multiseriate filaments ("trichomes") extending from cell wall at acropetal end.

Twenty-four species, southern Mexico and Antilles to Peru, Bolivia, and southeastern Brazil, in moist to wet forest zones at 0–2400 m.

In his generic description of *Saldanha*, Vellozo described the calyx as five-parted with subulate lobes, the corolla as five-lobed, and the stamens as six. He named two species, *S. illustris* Vell. and *S. nobilis*. The identities of both species are clear (Steyermark, 1972). Both of them typically have six calyx and corolla lobes and six stamens; the generic description thus applies equally well (or poorly) to each of them. Although Vellozo's generic description is somewhat weighted toward *S. illustris*, his description and illustration of a plant with five calyx and corolla lobes are either inaccurate, or depict an atypical individual. His illustration and description of *S. nobilis* accurately depict *H. parasitica*, and that species is therefore chosen as the lectotype.

KEY TO THE SUBGENERA OF *HILLIA*

- 1a. Corollas salverform, white or pale green, sometimes pink on surfaces exposed in bud.
  - 2a. Corolla lobes 5–6; stigmas subcapitate to linear, 0.5–4 mm long, positioned above or below anthers.
    - 3a. Stamens inserted near top of corolla tube; stigmas subcapitate to shortly linear, 0.5–2 mm long, positioned just above anthers \_\_\_\_\_ 1. subgenus *Hillia*
    - 3b. Stamens inserted near middle of corolla tube; stigmas linear, 2–4 mm long, positioned below anthers \_\_\_\_\_ 2. subgenus *Andinae*
  - 2b. Corolla lobes 4; stigmas linear, 2–6 mm long, positioned below anthers \_\_\_\_\_ 3. subgenus *Tetrandrae*
- 1b. Corollas funnelform to tubular or inflated, green, green flushed with yellow, pink, orange, or dull purple, or salmon to bright red.
  - 4a. Corollas funnelform, green or green flushed with yellow, pink, orange, or dull purple \_\_\_\_\_ 4. subgenus *Illustres*
  - 4b. Corollas funnelform to tubular or inflated, salmon to bright red \_\_\_\_\_ 5. subgenus *Ravnia*

KEY TO THE SPECIES OF *HILLIA*

- 1a. Leaf blades narrowly elliptic to lanceolate, 3–4 times as long as wide, 0.6–3 cm long.
  - 2a. Leaf blades lanceolate, thickly coriaceous; plants of Peru and Ecuador \_\_\_\_\_ 7. *H. macbridei*
  - 2b. Leaf blades elliptic to narrowly elliptic, subcoriaceous to coriaceous; plants of Mexico to western Panama \_\_\_\_\_ 12. *H. panamensis*
- 1b. Leaf blades elliptic to suborbicular or obovate, less than 3 times as long as wide, 2–22 cm long.
  - 3a. Primary, secondary, and sometimes tertiary venation prominulous to prominent on abaxial leaf surface.
    - 4a. Primary, secondary, and tertiary venation prominent \_\_\_\_\_ 4. *H. bonoi*
    - 4b. Primary and secondary but not tertiary venation prominent or prominulous.
      - 5a. Bark coppery red, peeling and wrinkled in small circumferential rings, especially on young twigs \_\_\_\_\_ 5. *H. killipii*
      - 5b. Bark gray-brown or dull red-brown, not peeling or wrinkled in circumferential rings.
        - 6a. Leaf blades 4.5–10 cm long, 1.8–5 cm wide; corolla lobes 12–26 mm long \_\_\_\_\_ 1. *H. wurdackii*
        - 6b. Leaf blades 9–22 cm long, 3–10 cm wide; corolla lobes 35–90 mm long.
          - 7a. Corolla lobes 35–54 mm long \_\_\_\_\_ 2. *H. macrophylla*
          - 7b. Corolla lobes 75–90 mm long \_\_\_\_\_ 3. *H. macromeris*
  - 3b. Leaf venation plane or sometimes the midrib prominulous on abaxial leaf surface.
    - 8a. Leaf blades rounded to obtuse at apex.
      - 9a. Corollas salverform, lobes 4; stigmas 5–15 mm long, held below anthers.
        - 10a. Leaf blades subcoriaceous to coriaceous; capsules with well-developed ridges or wings to 1 mm high; Greater Antilles and southern Mexico to northern Nicaragua \_\_\_\_\_ 9. *H. tetrandra*
        - 10b. Leaf blades coriaceous, often thickly so; capsules smooth or with slight longitudinal ridging; southern Nicaragua to northeastern South America.
          - 11a. Corolla tubes 42–55 mm long; lobes 15–27 mm long \_\_\_\_\_ 10. *H. maxonii*
          - 11b. Corolla tubes 35–40 mm long; lobes 8–12 mm long \_\_\_\_\_ 11. *H. palmana*
      - 9b. Corollas funnelform, lobes 5–9; stigmas 1–2 mm long, held above anthers or exerted.
        - 12a. Leaf blades subcoriaceous; stigmas included, held 2–3 mm below top of corolla tube \_\_\_\_\_ 17. *H. saldanhae*
        - 12b. Leaf blades thickly coriaceous; style exerted 4–5 mm beyond top of corolla tube \_\_\_\_\_ 18. *H. foldatsii*
    - 8b. Leaf blades acute to acuminate at apex.
      - 13a. Leaf venation subpalmate, with all secondary veins arising below middle of blade.
        - 14a. Corolla tubes red, ca. 38 mm long, the lobes 2.5 mm long; plants of southern Mexico \_\_\_\_\_ 20. *H. oaxacana*

- 14b. Corolla tubes green to yellow-green, 28–39 mm long, lobes 6–7 mm long; plants of Amazonian South America ..... 16. *H. ulei*
- 13b. Leaf venation pinnate, with at least one pair of secondary veins arising distal to middle of blade.
- 15a. Leaves strongly anisophyllous, the larger leaf at a node at least 1.5 times as long as the shorter leaf ..... 24b. *H. triflora* var. *pittieri*
- 15b. Leaves isophyllous or slightly anisophyllous, the larger leaf at a node less than 1.4 times as long as the shorter leaf.
- 16a. Calyx limb 36–68 mm long, with tube 33–56 mm long; leaf blades rounded to slightly cordate at base ..... 19. *H. costanensis*
- 16b. Calyx limb 3–36 mm long and lobed to base, minute and truncate to dentate, or lacking; leaf blades rounded to attenuate at base.
- 17a. Flowers (1–)3; corollas tubular to slightly inflated, red ..... 24a. *H. triflora* var. *triflora*
- 17b. Flowers solitary(–3); corollas salverform or funnellform, white or green or orange-red.
- 18a. Calyx lobes narrowly triangular to linear, 18–36 mm long ..... 23. *H. rivalis*
- 18b. Calyx lobes lacking or triangular to oblanceolate, orbicular, or ligulate, 3–35 mm long.
- 19a. Corollas salverform, white or pale green, sometimes pink on surfaces exposed in bud.
- 20a. Corolla lobes (5–)6(–9), the tubes (38–)60–125 mm long; plants of the Antilles and South America ..... 6. *H. parasitica*
- 20b. Corolla lobes 4, the tubes 45–75 mm long; plants of southern Mexico and Central America ..... 8. *H. loranthoides*
- 19b. Corollas funnellform, green to red-orange.
- 21a. Corollas red to orange; plants of Costa Rica and Panama.
- 22a. Corolla lobes 13–17 mm long; free portion of filaments 9–10 mm long ..... 22. *H. longifilamentosa*
- 22b. Corolla lobes 6–10 mm long; free portion of filaments ca. 1 mm long ..... 21. *H. allenii*
- 21b. Corollas green to yellow-green; plants of Costa Rica to South America.
- 23a. Leaf blades 4.5–6.5 cm long ..... 14. *H. psammophila*
- 23b. Leaf blades 8.5–15 cm long.
- 24a. Calyx limb 9–35 mm long, lobed to base ..... 15. *H. illustris*
- 24b. Calyx limb lacking or to 0.5 mm long, truncate to dentate ..... 13. *H. grayumii*

### 1. *Hillia* subg. *Hillia*.

*Calyx* limb lacking or with 5–6 lobes; *corollas* salverform, white or pale green on surfaces exposed in bud, sometimes flushed with pink or red, becoming yellowed with age, the lobes 5–6; *stamens* attached near apex of corolla tube; anthers subsessile; *stigmas* subcapitate to shortly linear, positioned just above anthers.

Seven species in the Antilles and South America.

1. *Hillia wurdackii* Steyermark, Mem. New York Bot. Gard. 23: 294. 1972. TYPE: Peru. Amazonas: Bongara, on road to La Rioja 5 km N of N end of Lake Pomacocha, 2000 m, 8 Oct. 1964, P. C. Hutchinson & J. K. Wright 6799 (holotype, VEN not seen; iso-

types, F, K not seen, MO, NY, UC not seen, US, USM not seen).

Shrubs or small trees to 7 m tall; bark gray-brown to red-brown, smooth. Leaf blades elliptic to somewhat ovate, 4.5–10 cm long, 1.8–5 cm wide, acuminate at apex with tip 5–10 mm long, cuneate to broadly obtuse at base, chartaceous; secondary veins pinnate, 4–8 pairs, midrib and secondary veins somewhat impressed adaxially, prominent abaxially, without domatia; margins flat; petioles 6–11 mm long; stipules 14–40 mm long, 6–18 mm wide, sometimes becoming red. Flowers solitary; peduncles 1–1.5 mm long; bracts lacking or ca. 3 × 1 mm; calyx limb lacking; corollas white or pale green on surfaces exposed in bud, the tubes 40–58 mm long, the lobes 5–6, (12)20–26 mm

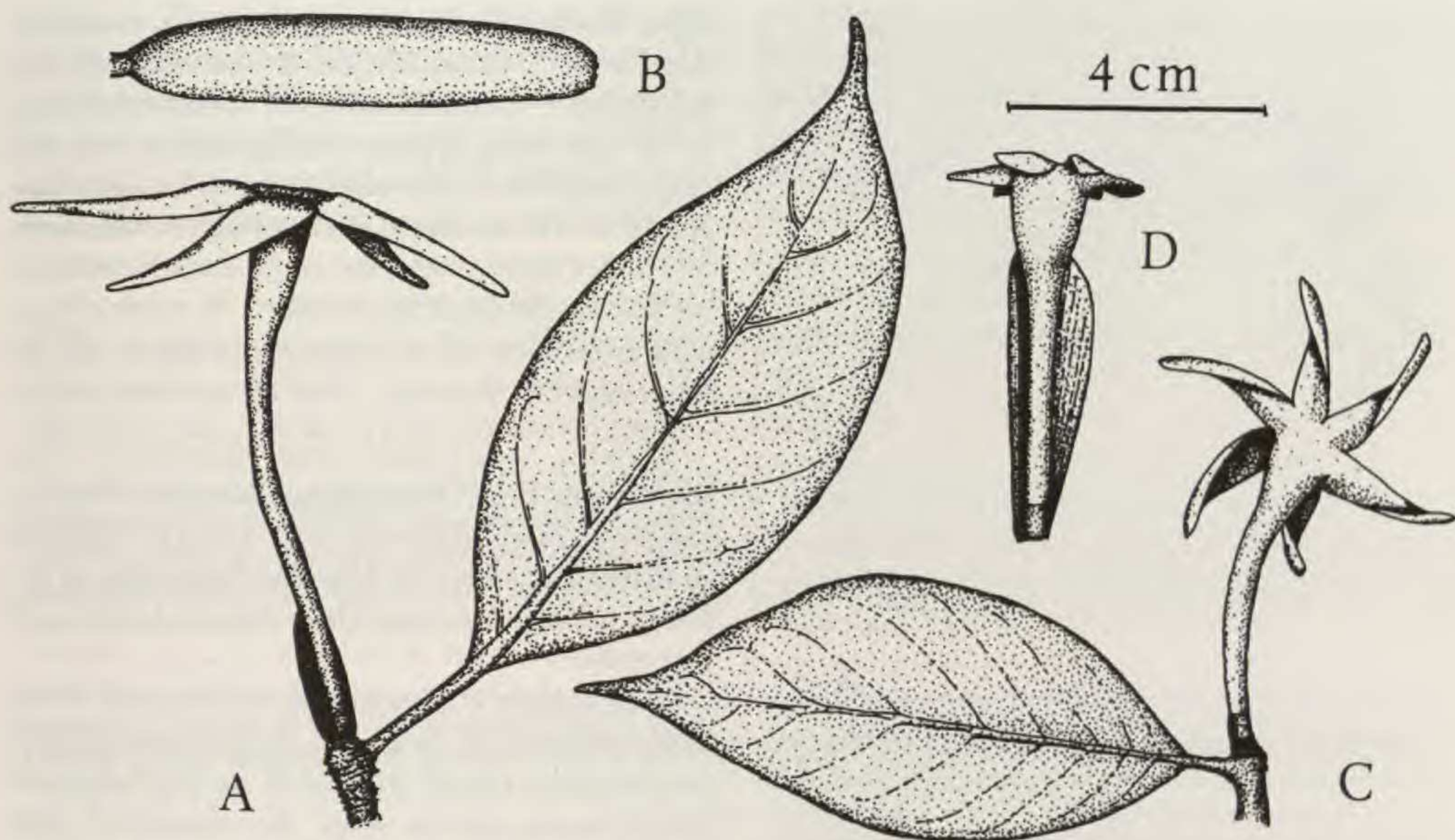


FIGURE 5. A, B. *Hillia killipii* Standl.—A. Habit with flower.—B. Capsule. C, D. *Hillia wurdackii* Steyerl.—C. Habit with flower.—D. Flower with stipule (floral). A, from Killip & Smith 26085 (NY); B, from Camp E-2405 (US); C, from Hutchison et al. 6799 (MO); D, from Woytkowski 8236 (MO). All to same scale.

long, 9–12 mm wide, elliptic to triangular, acute; anthers 5–6, subsessile, 10–11 mm long, with tips positioned 3–5 mm below top of corolla tube; ovary 5–10 mm long; stigmas subcapitate, 2–3 mm long, positioned immediately above anthers. Capsules 6.5–8 cm long including beak 6–7 mm long, 1–1.3 cm diam., not stipitate, smooth; seeds ca. 2 × 0.8 mm, with filaments 12–13 mm long. Figure 5C, D.

*Habitat, phenology, and distribution* (Fig. 3). Ecuador and Peru, in wet forests at 2000–2400 m. Collected in flower in June and October.

*Hillia wurdackii* is similar to *H. macrophylla*, *H. macromeris*, and *H. killipii* in its chartaceous to coriaceous leaves with the secondary veins prominent on the abaxial surface, but differs from the first two species in its smaller flowers and from the last in its smooth bark. This species may be only a small-flowered variant of *H. macrophylla*.

One collection, Woytkowski 8236 (Fig. 5D), is classified here provisionally but differs from other collections of *Hillia wurdackii* in its relatively short corolla lobes, only 12 mm long.

*Additional specimens examined.* ECUADOR. **Pastaza:** trail to Colonia 24 de Mayo, 2.5 km W on road from Puyo–Tena road at Km 9, 1°25'S, 77°58'W, Stein & Tucker 3108 (MO). PERU. **Amazonas:** Prov. Bongara, 4 km N of Pomacocha on road to Rioja, 5°40'S, 77°22'W, Knapp et al. 7497 (MO); Pomacocha, Vil-

caniza, Sagástegui 5997 (US); Mendoza, Woytkowski 8236 (MO); hills 1–5 km SSE (150°) of Yambrasbamba, Wurdack 1027 (US, photo NY). **Cajamarca:** Prov. Cutervo, distrito San Andrés, San Andrés–Chorro Blanco, El Suro, Sánchez 317 (MO).

**2. *Hillia macrophylla*** Standley, Publ. Field Columbian Mus., Bot. Ser. 7: 201. 1931. TYPE: Ecuador. Chimborazo: base of Mt. Chimborazo, 900 m, June & Aug. 1860, R. Spruce 6186 (holotype, K, photo K, F; isotype, F).

*Hillia marcano-bertii* Steyerl., Pittiera 9: 5. 1981. TYPE: Venezuela. Táchira: municipio Lobatera, Parque “Cazadero,” carretera Palo Grande–Minas de Carbón de Lobatera, 6 Dec. 1979, L. Marcano-Berti & I Peña 519-979 (holotype, VEN; isotype, MER not seen).

Suffrutescent herbs, shrubs, or small trees to 7 m tall; bark gray-brown to red-brown, smooth. Leaf blades elliptic to broadly elliptic-oblong or somewhat ovate, 9–22 cm long, 4.5–10 cm wide, acute to usually acuminate at apex with tip 5–10 mm long, cuneate to obtuse at base, chartaceous to coriaceous, sometimes pale abaxially; secondary veins pinnate, 6–8 pairs, midrib and secondary veins plane adaxially, prominent abaxially, sometimes with domatia; margins flat; petioles 6–20 mm long; stipules subtending flowers 22–76 mm long, 12–25 mm wide, sometimes becoming red. Flowers solitary; peduncles 1.5–2 mm long; bracts

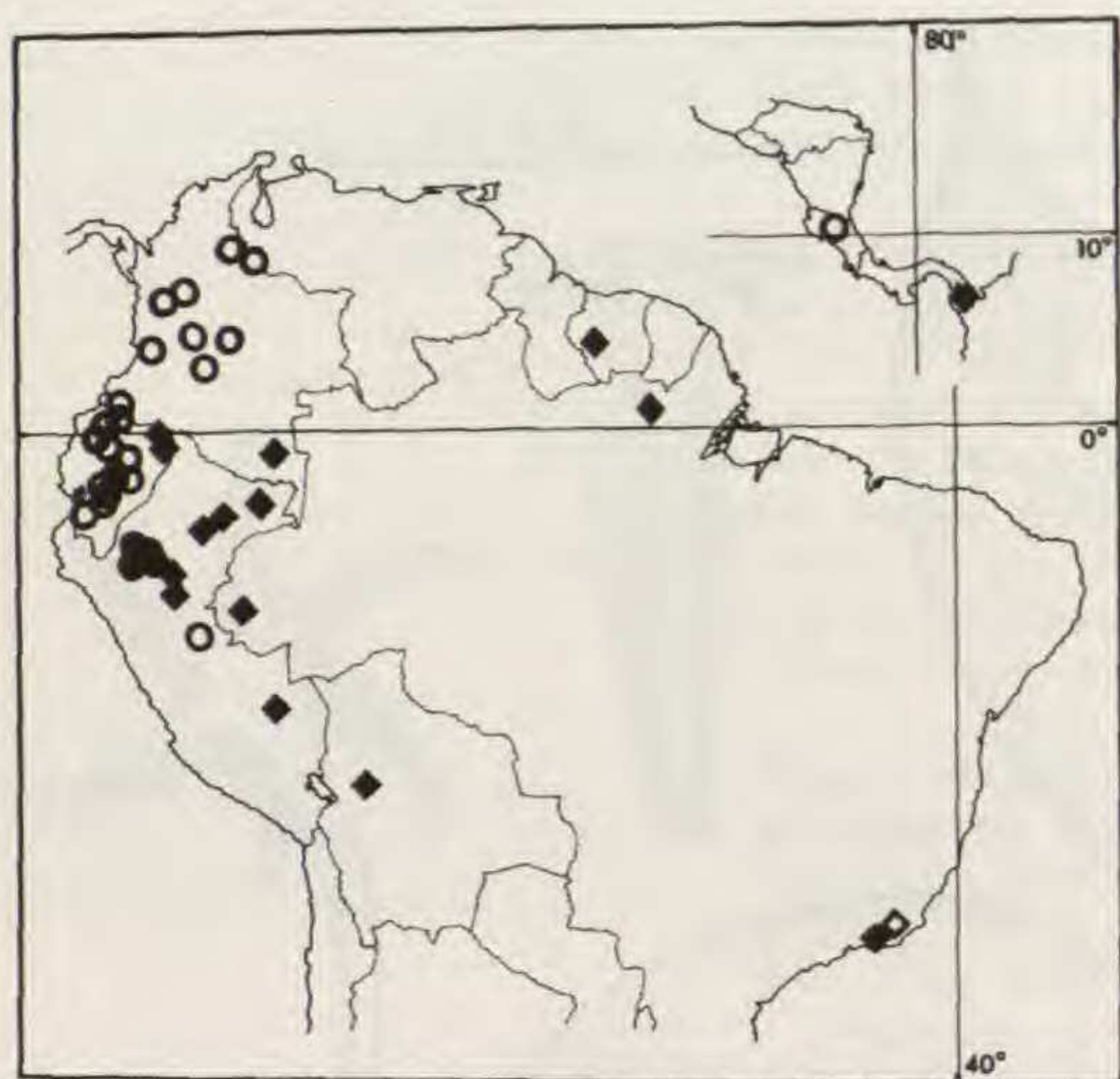


FIGURE 6. Distribution of *Hillia wurdackii* Steyerl. (solid circles), *H. macrophylla* Standl. (open circles), *H. ulei* K. Krause (solid diamonds), and *H. saldanhaei* K. Schum. (open diamond) in Central and South America.

lacking or  $1.5-11 \times 1.5-5$  mm; calyx limb lacking; corolla salverform, white or pale green on surfaces exposed in bud, the tubes 85-112 mm long, the lobes 5-6, 35-54 mm long, 6-12 mm

wide, triangular to narrowly triangular, acute; anthers 5-6(7), subsessile, ca. 8 mm long, with tips positioned 1-2 mm below top of corolla tube; ovary 5-10 mm long; stigmas subcapitate, 2-2.5 mm long, positioned immediately above anthers. Capsules 6.5-10 cm long including beak 1-5 mm long, 8-13 mm diam., not stipitate, smooth or with ca. 10 low longitudinal ribs; seeds  $3-4 \times$  ca. 1 mm, with trichomes 12-17 mm long. Figure 7C, D; Steyerl (1981: fig. 1, as *H. marcano-bertii*).

*Habitat, phenology, and distribution* (Fig. 6). Costa Rica, Venezuela, Colombia, Ecuador, and Peru, in wet forests at 800-1500 m. Collected in flower December to July and September to October, in fruit January, May, July to August, and November.

This species is distinguished by its large leaves and corollas. It is similar to *Hillia wurdackii*, *H. macromeris*, and *H. killipii* in its chartaceous to subcoriaceous leaves with the secondary veins prominent. Of these only *H. macromeris* has leaves of similar size, but it also has flowers about twice as large as those of *H. macrophylla*.

The only characteristics that would separate *Hillia marcano-bertii* are "pustulose" bark (which appears rather lenticellate in Steyerl's illus-

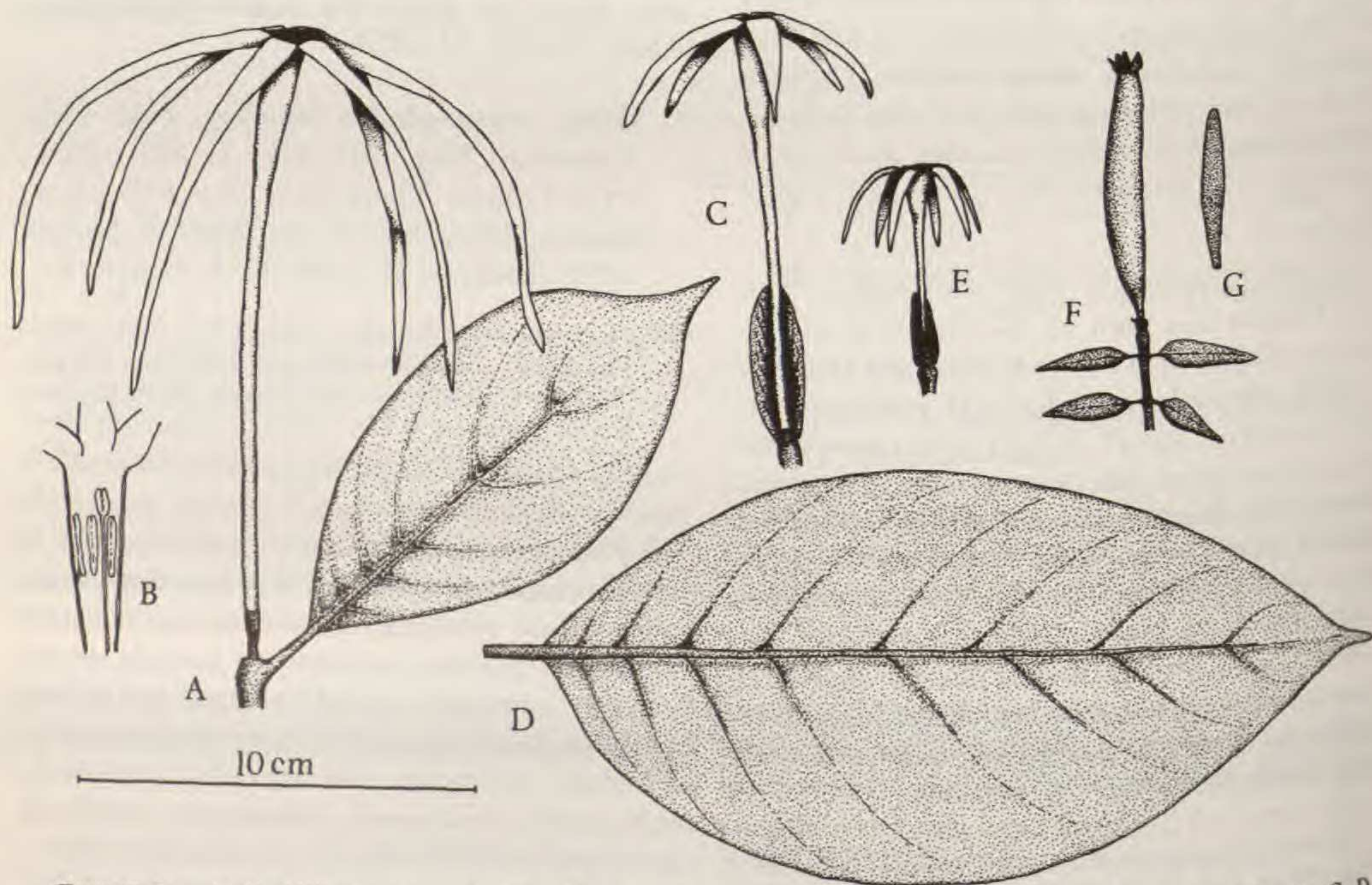


FIGURE 7. A, B. *Hillia macromeris* Standl.—A. Habit with flower.—B. Flower opened near top of tube. C, D. *Hillia macrophylla* Standl.—C. Flower with stipule (floral).—D. Leaf. E-G. *Hillia macbridei* Standl.—E. Flower with stipule (floral).—F. Habit with capsule.—G. Stipule (vegetative). A, B, from Lehmann BT 416 (NY); C, D, from Jativa & Epling 285 (NY); E, from Zak 3788 (MO); F, G, from Schunke 436 (F). A-F to same scale, G to twice this scale.



tration), a "verrucose" abaxial leaf surface, and corolla lobes that are broader by about 3 mm. The corolla lobes of *Hillia* species may vary widely in size, and additionally are usually strongly rolled at anthesis, so their unrolled width is difficult to measure. The occurrence of pustulose bark and verrucose leaf surfaces in some specimens is well within the range of variation seen in other species of *Hillia*. A similar geographic disjunction is seen in other species of *Hillia*, e.g., *H. macrophylla*. Therefore, this species is not maintained here.

*Representative specimens examined.* COSTA RICA. **Puntarenas:** Upala, El Pilón, cabeceras del Río Celeste, 10°49'N, 84°57'W, *Herrera 1320* (MO). COLOMBIA. **Antioquia:** municipio Guatepe, ca. 8 km NNE of Guatepe, vereda Santa Rita, Finca Montepinar, 6°17'N, 78°08'W, *Zarucchi 4168* (MO). **Boyacá:** vertiente oriental de la cordillera Oriental, terraza a lo largo del río Sacameño, *Jarmillo & van der Hammen 2748A* (COL). **Chocó:** Quibdó-Medellín road, 59 km W of La Mansa, *Gentry & Rentería 24168* (COL, MO). **Cundinamarca:** al S de Santandercito, laguna de Catarnica, 40 km SO de Bogotá, *Uribe 3197* (COL, US). **El Valle:** Cordillera Occidental, vertiente occidental, hoyo del río Digua, río San Juan, abajo de Queremal a la derecha del río entre Kms 52-53, *Cuatrecasas 23963* (COL, F, US). **Meta:** Cordillera La Macarena, extremo NO, macizo Renjifo, *Irobo & Schultes 1059* (MO, US). **Nariño:** Reserva La Planada, 1°10'N, 77°58'W, *Restrepo 449* (MO), *de Benavides 9602* (MO), 1°05'N, 78°01'W, *Gentry et al. 60342* (MO). **Norte de Santander:** Cordillera Oriental, región del Sarare entre el Alto del Loroy y el Alto de Santa Inés, *Cuatrecasas et al. 12398* (F, GH). ECUADOR. **Azuay:** between Río Blanco and Río Norcay on road between Chacanceo and Molleturo, *Steyermark 52827* (F). **Cañar:** quebrada W of San Miguel near Hacienda Monte Negro, *Játiva & Epling 285* (NY). **Carchi:** environs of Chical 12 km below Maldonado on Río San Juan, 1°04'N, 78°17'W, *Madison et al. 4519* (F). **Cotopaxi:** 3 km E of El Palmar on Quevedo-Latacunga road, *Dodson & Gentry 10195* (MO). **El Oro:** 11 km W of Piñas on new road to Santa Rosa, *Dodson & Gentry 9136* (MO). **Imbabura:** Cordillera Occidental, trail to San Luis de la Vega, *Drew E-553* (NY, US). **Napo:** ridge SE of Chaco across Quijos River below Baeza, *Ownbey 2669* (F, US). **Pastaza:** trail to Colonia 24 de Mayo, 2.5 km W on road from main Puyo-Tena road at Km 9, 1°25'S, 77°58'W, *Stein & Tucker 3108* (MO). **Pichincha:** old Quito-Santo Domingo road, 2-9 km NE of turnoff to old road out of Alluriquín, 00°20'S, 78°55'W, *Luteyn et al. 8738* (AAU, CAS, NY). PERU. **Huánuco:** distrito Chinchao, Bosque Nacional de Iparia, a lo largo del río Pachitea cerca del campamento Miel de Abeja, cerca 20 km arriba de la confluencia con el río Ucayali, *Schunke 5247* (F).

3. *Hillia macromeris* Standl., Publ. Field Columbian Mus., Bot Ser. 7: 22. 1930. TYPE: Colombia. Cauca: forests of Santa María on Río Timbiquí, Sep. 1903, *F. C. Lehmann (Brother Thomas) 416* (holotype, NY, photos A, F; isotypes, F, K, photo of K sheet NY).

Shrubs or trees to 7 m tall or occasionally lianas; bark gray-brown to red-brown, smooth. Leaf blades elliptic to somewhat ovate, 10-19 cm long, 3-9 cm wide, acute to acuminate at apex with tip 1-2 cm long, cuneate to rounded at base, chartaceous to subcoriaceous; secondary veins pinnate, 5-8 pairs, midrib and secondary veins plane adaxially, prominulous to prominent abaxially, without domatia; margins flat; petioles 8-16 mm long; stipules 32-70 mm long, 7-13 mm wide. Flowers solitary; peduncles ca. 2 mm long; bracts lacking; calyx limb lacking; corollas salverform, white, the tubes 14.5-15 cm long, the lobes 6, 7.5-9 cm long, ca. 5 mm wide, very narrowly triangular, acute to attenuate; anthers 6, subsessile, 7-14 mm long, with tips positioned 12-15 mm below top of corolla tube; ovary 5-10 mm long; stigmas shortly linear, ca. 5 mm long, positioned immediately above anthers. Capsules ca. 11 cm long including beak 1-5 mm long, ca. 12 mm diam., not stipitate, smooth or with 8-10 low longitudinal ribs; seeds ca. 2 × 0.5 mm, with filaments ca. 10 mm long. Figure 7A, B.

*Habitat, phenology, and distribution* (Fig. 8). Colombia to Peru, in wet forests at 100-1890 m. Collected in flower in May, September, and November, in fruit in November.

This species is distinguished by its very long corolla tube and lobes, about 50% larger than those of any other species of *Hillia*. It is similar to *H. wurdackii*, *H. macrophylla*, and *H. killipii* in its chartaceous to coriaceous leaves with the secondary veins prominent on the abaxial surface. Of these only *H. macrophylla* has leaves of similar size, but it has flowers about half as large.

*Additional specimens examined.* ECUADOR. **Carchi:** along the Río Verde, at trail to Rafael's Mountain Finca, 0°52'N, 78°08'W, *Hoover 1920* (MO). **Morona-Santiago:** 6 km E of Limo on road (under construction) to La Unión, *Harling & Andersson 24490* (GB). PERU. **Amazonas:** near Shaim above Quebrada Nahim, 1 day's walk from Huampami, Río Cenepa, *Berlin 429* (MO). **Loreto:** Prov. Maynas, Yanamono, Explorama Lodge, 3°30'S, 72°50'W, *Vásquez & Jaramillo 4116* (MO). **San Martín:** Prov. Mariscal Cáceres, distrito Tocache Nuevo, Río de la Plata, NE of Tocache, *Schunke 8380* (MO).

4. *Hillia bonoi* Steyermark, *Ernstia* 42: 5. 1987. TYPE: Venezuela. Táchira: distrito Junín, entre Rubio y Las Delicias, 2000 m, 2 Apr. 1984, *J. Bono 3797* (holotype, VEN not seen, photo MO).

Shrubs to ca. 1 m tall; bark smooth, gray-brown to red-brown. Leaf blades broadly elliptic to somewhat ovate, 14.5-16.8 cm long, 9-10.8 cm wide,

acuminate at apex with tip 1–1.5 cm long, obtuse to rounded at base, stiffly subcoriaceous to coriaceous; secondary veins pinnate, ca. 10 pairs, midrib, secondary, and tertiary veins impressed adaxially, prominent abaxially, sometimes with domatia; margins flat to somewhat revolute; petioles 15–28 mm long; stipules subtending flowers ca.  $38 \times 12$  mm. Flowers solitary, subsessile; bracts not seen; calyx limb not seen; corollas salverform, white, the tubes ca. 7 cm long, the lobes 5, ca. 3 cm long, ca. 1 cm wide, narrowly lanceolate to triangular, acute; anthers 5–6, subsessile, with tips positioned 2–3 mm below top of corolla tube; stigmas subcapitate, ca. 2–3 mm long, positioned immediately above anthers. Capsules not seen.

*Habitat, phenology, and distribution.*

Known only from the type locality, in cloud forest at 2000 m. Collected in flower in April.

This species can be distinguished by its leaves, which are larger and proportionally wider than those of most other species of *Hillia*, with the secondary and higher-order venation impressed above and prominent on the lower surface.

5. ***Hillia killipii*** Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 159. 1930. TYPE: Peru. Junín: Pichis trail between San Nicolás and Azupizu, 650–900 m, 6 July 1929, *E. P. Killip & A. C. Smith* 26085 (holotype, F, photo F; isotypes, NY, US).

Shrubs or small trees to 5 m tall or sometimes lianas; bark of young twigs coppery red, papyraceous, and wrinkled in circumferential rings, becoming gray-brown and smooth or peeling on older stems. Leaf blades elliptic, 7.8–12.5 cm long, 3–5 cm wide, acuminate at apex with tip 5–10 mm long, acute to obtuse at base, chartaceous; secondary veins pinnate, 5–6 pairs, midrib and secondary veins smooth adaxially, prominent abaxially, without domatia; margins flat; petioles 8–17 mm long; stipules 17–27 mm long, 4–9 mm wide. Flowers solitary; peduncles 1–2 mm long; bracts lacking; calyx limb lacking; corollas salverform, white or pale green on surfaces exposed in bud, the tubes 53–80 mm long, the lobes 5–6, 33–48 mm long, 3–8 mm wide, narrowly triangular, acute; anthers 5, subsessile, 6–7 mm long, with tips positioned 6–7 mm below top of corolla tube; ovary 5–10 mm long; stigmas shortly linear, ca. 5 mm long, positioned immediately above anthers. Capsules 7–10 cm long including beak 1–5 mm long, ca. 8–10 mm diam., not stipitate, smooth or with ca. 10 low longitudinal ribs; seeds 2–5 × 0.8–1 mm, with filaments 10–25 mm long. Figure 5A, B.

*Habitat, phenology, and distribution* (Fig. 8). Peru and Ecuador, in wet forests at 600–1600 m. Collected in flower in January, April, and July to September, in fruit March, April, and July.

This species can be recognized by its chartaceous leaves with secondary veins prominent on the abaxial surface and coppery red, papery bark that is circumferentially wrinkled and sometimes peeling.

*Representative specimens examined.* ECUADOR. **Napo:** region of Archidona-Tena along Río Pano at foot of Cordillera de Guacamayos W of Tena, *Ownbey* 2737 (F, US). PERU. **Cuzco:** Río Arasa NE of Cuzco, *Sandeman* 3672 (F). **Loreto:** Pumayacu between Balsapuerto and Moyobamba, *Klug* 3145 (A, F, GH, US). **San Martín:** Prov. Rioja, Pedro Ruíz–Moyobamba road, Km 390, 5°50'S, 77°45'W, *Smith* 4385 (MO).

6. ***Hillia parasitica*** Jacquin, Enum. Pl. Carib. 18. 1760; Select. Stirp. Am. 96, t. 66. 1763. TYPE: Martinique, *Jacquin s.n.* (holotype, BM not seen; cited by Moore & Rendle, 1936).

*Hillia longiflora* Sw., Prodr. 58. 1788, nom. inval., pro syn.

*Cosmibuena acuminata* Ruiz & Pav., Fl. Peruv. 3: 4, t. 226. 1802. TYPE: Peru. Huánuco: Chicoplaya, 1798, *J. Tafalla* 15/24 (holotype, MA not seen, photos F, GH, MO; isotype, F).

*Saldanha nobilis* Vell., Fl. Flum. 142. t. 3: 158. 1825. *Hillia parasitica* var. *nobilis* (Vell.) Steyererm., Mem. New York Bot. Gard. 23: 292. 1972. TYPE: Brazil. Rio de Janeiro region, Fl. Flum. t. 3: 158, lectotype designated here.

*Fereirea vellozoana* Schult. & Schult. f., Syst. Veg. 7: 83. 1829. TYPE: Fl. Lusit. Bras. Spec. t. 1, fig. 8, 1788, lectotype designated here.

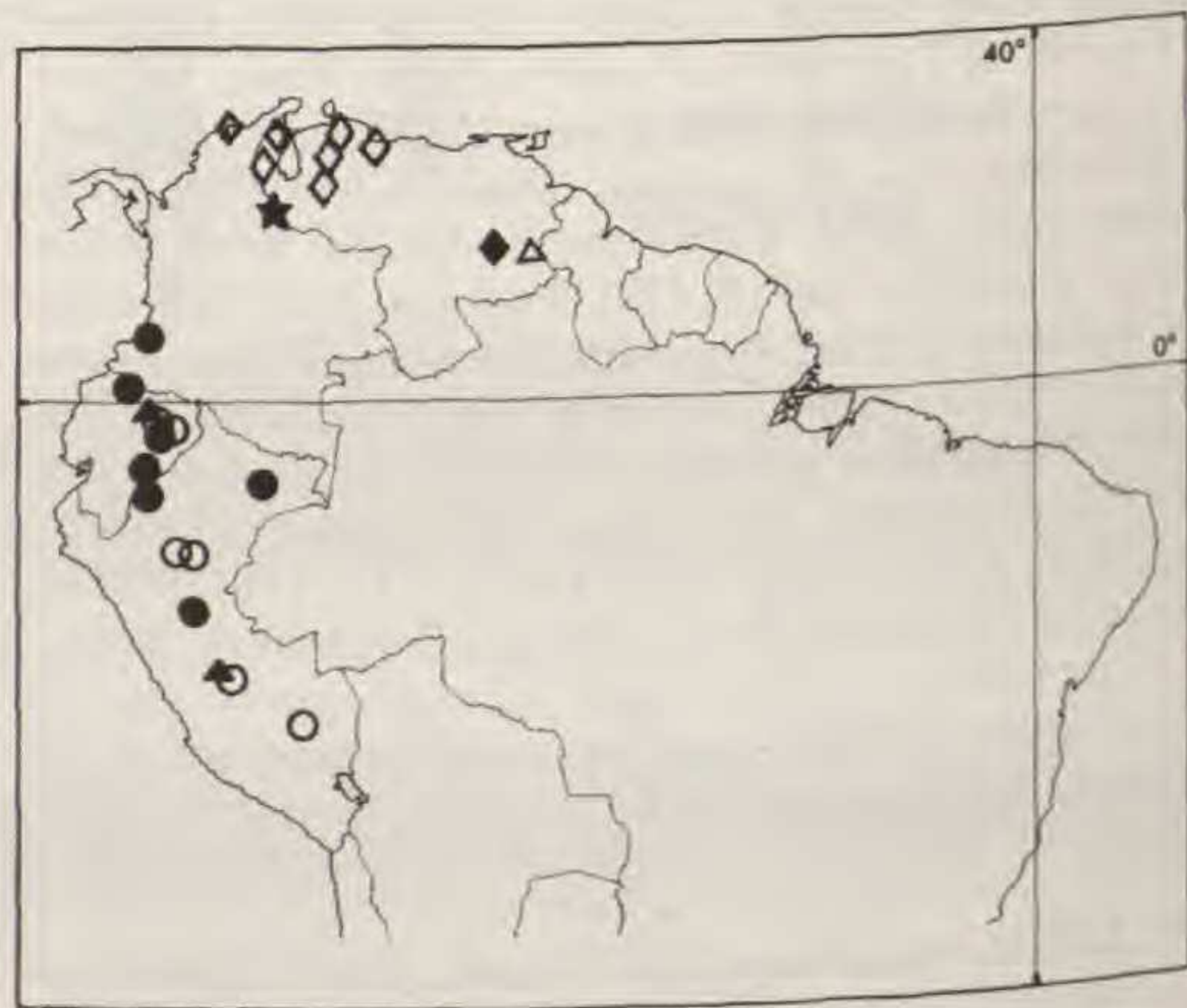


FIGURE 8. Distribution of *H. bonoi* Steyererm. (star), *H. macromeris* Standl. (solid circles), *H. killipii* Standl. (open circles), *H. macbridei* Standl. (solid triangles), *H. psammophila* Steyererm. (open triangle), *H. foldatsii* Steyererm. (solid diamond), and *H. costanensis* Steyererm. (open diamonds) in South America.

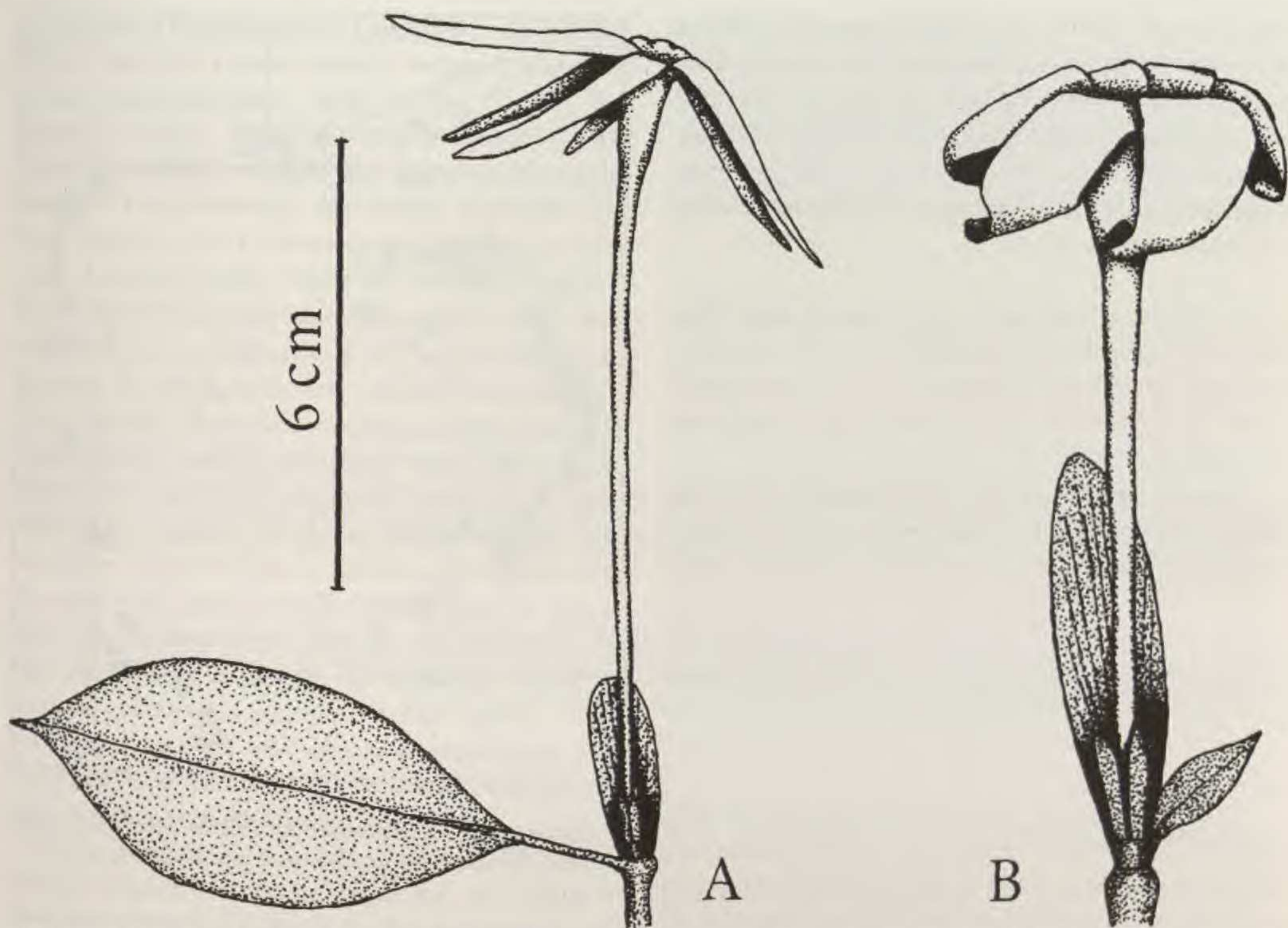


FIGURE 9. A, B. *Hillia parasitica* Jacq.—A. Habit with flower, “typical” form from the Antilles and eastern South America.—B. Habit with flower, “nobilis” form from northwestern South America. A, from Otero 639 (MO); B, from Stein & Cogollo 3564 (MO). A, B to same scale.

- Hillia brasiliensis* Cham. & Schtdl., *Linnaea* 4: 201. 1829. TYPE: Brazil. Brasilia aequinoctiali, Sellow 1754 (holotype, B destroyed; isotypes, P, US).
- Posoqueria montana* Mart., *Flora* 24, Beibl. 2: 80. 1841. TYPE: Brazil. Minas Gerais: in sylvis montanis ad Villa Rica, April, *Oreas s.n.* (holotype, W not seen).
- Hillia boliviana* Britton, *Mem. Torrey Bot. Club* 3: 43. 1893. TYPE: Bolivia. Cochabamba: Yungas, 1890, A. M. Bang 660 (holotype, NY; isotypes, F, GH, NY, US).
- Hillia odorata* K. Krause, *Bot. Jahrb. Syst.* 40: 321. 1908. TYPE: Peru. Junín: Prov. Tarma, prope Huacapistana, 1800 m, 14 Jan. 1903, A. Weberbauer 2152 (holotype, B destroyed, photos F, GH, MO, NY; isotype, F).
- Hillia weberbaueri* Standl., *Field Mus. Nat. Hist., Bot. Ser.* 11: 214. 1936. TYPE: Peru. Without locality, 1909–1914, A. Weberbauer 6955 (holotype, F, photo F).
- Hillia maguirei* Steyerm., *Mem. New York Bot. Gard.* 10(5): 209, fig. 73a–d. 1964. TYPE: Venezuela. Amazonas: Serranía Yutaje, Río Manapiare, Cerro Yutaje, 1750 m, 17–19 Feb. 1953, B. Maguire & C. K. Maguire 35287 (holotype, NY; isotypes, GH, P not seen, US).
- Hillia microcarpa* Steyerm., *Mem. New York Bot. Gard.* 23: 292. 1972. TYPE: Venezuela. Mérida: steep NW- and NE-facing slopes above “La Isla,” above Tabay, 2285–2745 m, 18 May 1944, J. A. Steyermark 56591 (holotype, F, photo NY).

Suffrutescent herbs, shrubs, or small trees to 8

m tall; bark gray-brown to red-brown, smooth. Leaf blades elliptic to elliptic-oblong, 3.4–13 cm long, 1.7–6.5 cm wide, acute to usually acuminate at apex with tip 5–10 mm long, cuneate to acute at base, subcoriaceous to coriaceous; secondary veins pinnate, (2–)4–8(–9\*) pairs, plane or sometimes midrib prominulous abaxially, without domatia; margins flat; petioles (2–)4–22 mm long; stipules 9–55 mm long, 4–14 mm wide, sometimes red. Flowers solitary; peduncles 1–4 mm long; bracts lacking or 2–7(–9\*) × 1–4 mm; calyx limb lacking or divided to base, the lobes (5–)6(–9), 3–12 mm long, 0.8–6 mm wide, narrowly triangular to ligulate or orbicular, acute to rounded; corollas salverform, white or sometimes pale green or pink on surfaces exposed in bud, the tubes (38\*–)60–125 mm long, the lobes (5–)6, 15–60 mm long, 4–12 mm wide, triangular to lanceolate, obtuse to acute; anthers (5–)6, subsessile, 4.5–8 mm long, with tips positioned 2–3 mm below top of corolla tube; ovary 5–10 mm long; stigmas subcapitate, 1–2 mm long, positioned immediately above anthers. Capsules 3–11.5(–20) cm long including beak 1–5 mm long, 6–10(–12\*) mm diam., not stipitate, smooth; seeds 2–4 × 0.5–1 mm, with filaments 8–15 mm long. Figure 9; Andersson & Persson (1991: fig. 2C,

D); Howard (1989: fig. 188); Lamarck (1792: t. 257, fig. 1); Moore & Rendle (1936: fig. 3); Robbrecht (1988: figs. 58, 59); Roemer (1796: t. 6, fig. 8); Sastre & Portecop (1985: fig. 220); Schumann (1889: fig. 111; 1891: fig. 19P-R); Sims (1804: fig. 721); Steyermark (1974: fig. 21); Swartz (1791: t. 5, fig. 1).

*Habitat, phenology, and distribution* (Fig. 10). Throughout the Antilles and most of mainland tropical South America, in wet forests at 200–2400 m. Collected in flower and in fruit throughout the year.

This species is common and variable. It is distinguished by its leaf blades with acute to usually acuminate apices and the secondary venation plane and usually not evident, and usually 6-merous corollas with tubes 60–125 mm long and lobes 15–60 mm long. Measurements cited by Steyermark (1972, 1974) but not observed on material studied are designated with asterisks (\*) in the description above.

*Hillia parasitica* varies in several features that seem uncorrelated with geographic distribution. Leaf size may vary even on a single plant, but in general appears to be correlated with habitat: plants from wet windy ridges and high montane areas tend to have smaller leaves than plants from lower, drier, or more sheltered sites. The venation is usually plane, although the midrib may be prominulous abaxially in plants from South America, particularly on relatively large leaves. Secondary venation is more evident on some collections than others, apparently due as much to treatment of the specimens with formalin or alcohol as to any inherent feature of the plants.

The shape of the corolla lobes in *Hillia parasitica* varies from narrow in the Antilles and northeastern South America to relatively broad in the southwestern part of its range, but the variation is continuous and does not appear to be correlated with any other feature. The lengths of the corolla tube and lobes also vary, but within-population ranges are frequently as wide as differences among plants from widely different sites. Plants from the tops of tepuís tend to have relatively shorter corollas, but these do not fall outside the range of corolla size represented in other areas. Occasional plants from both the Antilles and the mainland lack a calyx limb, as do other species of *Hillia*. Tepuís plants with relatively short corollas and no calyx limb were segregated by Steyermark as *H. maguirei*, but when the collection locality is not known these plants cannot be segregated and this species is not maintained here. When present, the calyx



FIGURE 10. Distribution of *Hillia parasitica* Jacq. (solid circles) in the Antilles and South America.

lobes in *H. parasitica* vary in shape from triangular to elliptic throughout most of the geographic range, to broadly ligulate or orbicular in some plants from scattered localities in Amazonian Venezuela and Colombia. Steyermark segregated plants with broadly ligulate to orbicular calyx lobes as *H. microcarpa*, based on both this feature and relatively small flowers. However, comparable variation in the shape of the calyx lobes is seen in other species of *Hillia* from several subgenera, and the flowers fall within the normal range for *H. parasitica*. No other features distinguish *H. microcarpa*, and it is not maintained here.

The stipules subtending the flowers range in length from 14 to 30 mm in the Antilles, from 15 to 40 mm in northern and eastern South America, and from 25 to 74 mm in western South America. Plants of western South America with relatively long floral stipules that tend to persist until anthesis have been segregated as *Hillia boliviana*. However, the size range for the floral stipules of "*H. boliviana*" overlaps that found in plants from elsewhere, as does the degree of persistence, and this species is not maintained here.

Steyermark (1972) recognized two varieties of *Hillia parasitica*, variety *parasitica* and variety *nobilis*, based on corolla size, size of the stipules subtending the flowers, and form of the bracts ("bracteoles"). He gave the range of variety *nobilis*

as "southern Brazil, Bolivia, Colombia, and possibly Peru," with the typical variety occupying a more or less complementary range in the "Lesser and Greater Antilles, Mexico, Central America, and South America (Venezuela and Territorio Roraima, Brazil)." Unfortunately, the range of corolla and bract sizes he gave for variety *nobilis* also includes many Antillean plants, while the form of the bracts he attributed to variety *parasitica* does not fit most Antillean plants, and several of the measurements he gave for these taxa are contradicted in specimens that he annotated contemporaneously. The characters he used to separate these varieties do indeed vary over the geographic range of *H. parasitica*, but appear to do so independently. Examination of specimens he annotated suggests that the relatively broad corolla lobes found in plants from the southwestern part of the range of *H. parasitica* were probably the primary character used in practice to delimit variety *nobilis*. This variation in corolla lobe shape is continuous and uncorrelated with other characteristics; variety *nobilis* is not recognized here.

*Hillia parasitica* is weedy and common in the Antilles, where it may be epiphytic or rooted in saturated disturbed soils. It is also commonly collected in southeastern Brazil, but relatively few collections have been seen from Colombia, Ecuador, and Bolivia. Howard has suggested in notes accompanying specimens from Puerto Rico that there may be some incidence of "distyly or cryptic dioecy," but this has not been tested. His specimens show variation by several millimeters in the position of the stamens relative to the top of the corolla tube, similar to the variation found in other species, but the stigmas are held above the anthers in all specimens seen. The flowers are very strongly and sweetly fragrant during the night, beginning at about 6–7 P.M. in Puerto Rico, but are odorless during the day.

*Representative specimens examined.* BOLIVIA. **Cochabamba:** small power station ca. 80 mi. NE of Cochabamba, *Brooke* 6700 (F, NY). **La Paz:** Prov. Murillo, 44 km below Lago Zongo dam, vicinity of Cahua hydroelectric plant, 16°03'S, 68°01'W, *Solomon* 10826 (CTES, MO). **Santa Cruz:** Santa Cruz, *Williams* 1478 (F, NY, US). BRAZIL. **Bahia:** summit of Morro do Chapéu, ca. 8 km SW of town of Mdoch to W of road to Utinga, 11°35'S, 41°12'W, *Harley* 22773 (NY, US). **Ceará:** sitio Espírito Santo, Serra da Aratanha–Maranguapé, *Martens & Castro* 7076 (MO). **Espírito Santo:** Santa Leopoldina, cabeceira do Rio Bonito, divida com o municipio de Santa Teresa, *Boudet* 2280 (MO). **Minas Gerais:** mpio. Sêrro, Boca de Mata, *Williams & Assis* 7916 (F, GH). **Paraná:** Tacarchí, *Dusén* 16113 (A, F, GH, MO, NY). **Rio de Janeiro:** region of Itatiaia, *Ginzberger* 273 (F), *Hoehne* 11504 (F), *Plowman* 2862 (GH).

**Roraima:** summit of Serra de Lua, 2°25–29'N, 60°11–14'W, *Prance et al.* 9436 (F, NY). **Santa Catarina:** Mina Velha, Garura, San Francisco do Sul, *Reitz & Klein* 5789 (NY, US). **São Paulo:** Boracéia, Salisópolis, *Kuhlmann & Kühn* 1750 (F). COLOMBIA. **Antioquia:** Cordillera Central 7–15 km E of Sonsón on road to Nariño, 5°43'N, 75°15'W, *Stein & Cogollo* 3564 (COL, MO, NY). **Boyacá:** extreme western part of Mt. Chapón, *Lawrance* 351 (F, MO, NY). **Cauca:** La Depresión, foot of Cerro Pinche, *Core* 1327 (US). **Cundinamarca:** Cordillera Oriental, municipio San Bernardo, verde de Santa Rita, Alto de Buenos Aires, *Jaramillo et al.* 7072 (COL). **Huila:** Cordillera Oriental, E of Neiva, *Rusby & Pennell* 863 (NY). **Magdalena:** Sierra Nevada de Santa Marta, SW of Finca Los Arroyitos, 10°56'N, 73°58'W, *Kirkbride* 2398 (COL, NY, US). **Nariño:** entre Altaquer y Junín, Cuyambe, *Idrobo* 2356 (NY, US). **Santander:** Virolín a Charaló, *Romero & Jaramillo* 6753 (COL). CUBA. **Granma:** Río Guayabo above the falls, *Shafer* 3619 (F, NY, US). DOMINICA. Near Freshwater Lake and Laudat, *Smith* 10256 (A, NY, US), *Wilbur et al.* 7389 (F, MO, NY). DOMINICAN REPUBLIC. **Barahona:** al S de Baoruco, 4 km arriba del poblecito rural "Entrada de Cortico," en el camino al Gajo ("monteado Nuevo"), 18°07'30"N, 71°13'30"W, *Zanoni et al.* 18867 (NY). **El Seibo:** Los Haitises, cerca de la caseta de guardaparques en Monte Bonito, 19°00'N, 69°30'W, *Zanoni et al.* 35437A (NY). **La Vega:** Bonao, subido al Casabito, *Liogier & Liogier* 21526 (F, NY, US). **Peravia:** 14.2 km al N del Parque Central en San José de Ocoa en el camino a Carmena, zona rural "El Caliche," 18°37'N, 70°31'W, *Zanoni et al.* 19853 (NY). **Samaná:** vicinity of Laguna, Samaná Peninsula, chiefly on Pilon de Azúcar, *Abbott* 2357 (GH). **Santiago:** Cordillera Septentrional, Loma Diego de Ocampo, 19°34'30"N, 70°44'30"W, *Zanoni et al.* 26660 (NY). ECUADOR. **Carchi:** just below Tambo Bella Vista, pass between Río San Juan and Río Plata, *Steere* 8070 (F). **El Oro:** along trail between Portovelo and Río Cabra, passing Minas Nuevas and Huertas and arriving at Cachicarán, *Steyermark* 54093 (A, F). **Imbabura:** Río Lita below Buenos Aires, Cordillera Occidental, *Steere & Camp* 8196 (F). **Manabí:** San Sebastián, Machalilla National Park, 1°36'S, 80°42'W, *Gentry et al.* 72567 (MO). **Pichincha:** km 70, old road from Quito to Santo Domingo, *Dodson & Dodson* 11852 (MO). **Morona–Santiago:** Plan del Milagro, ca. 10 km NW of Indanza, *Jørgensen* 40 (F). **Sucumbios:** road in construction between Santa Bárbara and La Bonita, *Harling & Andersson* 12475 (US). **Tungurahua:** northern slopes of Volcán Tungurahua, *Dodson & Thien* 1875 (MO). FRENCH GUIANA. **Cayenne:** Montagnes de la Trinité, sommet nord-est, *de Granville* 5856 (MO, NY), 6215 (MO). GRENADA. Morne Quaqu, *Beard* 1225 (A, F, GH, MO, US). GUADELOUPE. Trois-Rivières, *Duss* 2546 (F, NY, US). HAITI. **Nord:** Massif du Nord, Anse-a-Faleur, Morne Chêneau, *Ekman* 4405 (GH, NY, US). **Sud:** Montagne de la Hotte, summit Morne Delour, *Eyerdam* 393 (GH, US). JAMAICA. **Surrey:** vicinity of Cinchona, near Vinegar Hill, *Britton* 219 (F, NY). MARTINIQUE. Deux-Choude du Lorrain, Mont Pelée, *Père Duss* 1462 (F, NY, US). MONTSERRAT. Summit of Castle Peak, English Crater, central mountain range, *Howard & Howard* 17553 (A). PERU. **Amazonas:** Prov. Bagua, 12 km E of La Peca, *Barbour* 2614 (MO). **Ayacucho:** Prov. Huamango, Tambillo, *de Jelski* 367 (MO). **Cuzco:** Prov. La Convención, 10 km walking NE from Hacienda Luisiana and the Apurimac River,

12°30'S, 73°30'W, *Dudley 10414* (F). **Huánuco:** ditto. Chinchao, camino a la Hacienda Derrepente, margen derecha del río Derrepente, *Schunke V. 5317* (COL, F, GH, NY, US). **Junín:** Chanchamayo valley, *Schunke 290* (F). **Loreto:** Divisoria, *Ferreyra 1666* (US), 2255 (US). **Pasco:** Prov. Oaxapampa, Río Chontabamba valley, 1–15 km from Oxapampa, 10°35'S, 75°30'W, *Smith 4139* (MO). **San Martín:** Prov. Mariscal Cáceres, Tocache Nuevo, río de la Plata, *Schunke V. 8170* (F, MO). PUERTO RICO. E slope of Luquillo Mountains, *Heller 4612* (A, F, GH, MO, NY, US); Cayey, Rte. 184, Cerro la Santa in Carite Reserve, *Taylor 6353* (UPRRP); Barranquitas, Cerro Torrecilla, *Alvarez & Rodríguez 24* (UPRRP); Mount Mandios near Jayuya, *Britton & Cowell 924* (F, NY); Monte Alegrillo, near Maricao, *Britton et al. 2591* (NY, US). SABA. Top of the mountain, *Arnoldo 3302* (A). ST. KITTS. Molyneaux Estate, *Britton & Cowell 697* (NY, US). ST. LUCIA. Gros Piton, *Beard 1163* (F, GH, MO, US). ST. VINCENT. Mount St. Andrews, *Eggers 6754* (A, US). TRINIDAD. Aripo road via Arima near bathing pool, Mile Posts 4, 5, *Broadway 5709* (F, MO). VENEZUELA. **Amazonas:** dept. Atabapo, slopes of Marahuaca, 1–2 km N of Sima Camp, 3°43'N, 65°31'W, *Liesner 18431* (MO, NY). **Aragua:** Pica hacia Cerro Periquitos, estación biológica Rancho Grande, *Aristeguieta 4239* (F, MO). **Bolívar:** Auyan-tepuí, *Cardona 207* (F, US), *Steyermark 93882* (NY), 94089 (NY), *Vareschi & Foldats 4771* (F). **Falcón:** ditto. Petit, Sierra de San Luis, Paraguariba, 3 km ENE of Cerro Galicia, 2–3 km N of Curimagua, 11°11'30"N, 69°41'W, *Plowman et al. 13370* (F). **Lara:** Parque Yacambú, beyond crest from Sanare, *Berry 3468* (MO). **Mérida:** between La Azulita and La Trampa on road to Lagunillas, *Steyermark 56156* (F). **Miranda:** Cerro del Bachiller, near E end, above Quebrada Corozal, S of Santa Cruz, 10 km by air W of Cúpira, 10°09'N, 65°48'W, *Steyermark & Davidse 116874* (MO). **Monaguas:** ditto. Acosta, serranía del Turumiquire, altiplanicie en la fila La Montaña, cabeceras del río Negro (afluente del río Colorado), 10°02'N, 63°52'O, *Huber et al. 6316* (NY, US). **Nueva Esparta:** Isla Margarita, San Juan Mountain, *Johnston 41* (F, GH, NY, US). **Portuguesa:** 50 km WNW of Guanare by air, 15–17 km N of Chabasquén, 9°28'N, 69°55'W, *Liesner et al. 12775* (MO). **Yaracuy:** 10 km N of Salom, top of Gamoletal, El Amparo, *Davidse et al. 20716* (MO, NY).

**2. Hillia subg. Andinae** C. M. Taylor, subg. nov. TYPE: *Hillia macbridei* Standl.

A *Hillia* subg. *Hillia* stigmatibus linearibus corolla infra medium positus differt.

*Calyx* limb divided to base, lobes 5–6; *corollas* carnose, salverform, white, lobes 5–6; *stamens* 5–6, attached near middle of corolla tube; anthers subsessile; *stigmas* linear, positioned below anthers.

One species, Ecuador to central Peru.

**7. Hillia macbridei** Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 277. 1929. TYPE: Peru. Junín: Hacienda Schunke, La Merced, ca. 4000 ft. [1290 m], 27 Aug.–1 Sep. 1923,

*J. F. Macbride 5670* (holotype, F, photos F, NY).

Suffrutescent herbs or shrubs to 1 m tall; bark gray-brown to red-brown, smooth. Leaf blades lanceolate, 1.8–3 cm long, 4–8 mm wide, acute at apex, rounded at base, coriaceous to usually stiff; secondary veins obscure, smooth or midrib sometimes prominulous abaxially, without domatia; margins frequently revolute; petioles 1–4 mm long; stipules 8–20 mm long, 1.5–6 mm wide. Flowers solitary; peduncles 1–1.5 mm long; bracts lacking or 1–2 mm long and wide; calyx limb divided to base, the lobes 5–6, triangular to lanceolate or elliptic, 1–5 mm long, 0.5–3 mm wide; corollas salverform, white, the tube 40–49 mm long, 1.5–2.5 mm diam., the lobes 5–6, 22–24 mm long, 2.5–4 mm wide, narrowly triangular to linear, acute; anthers 5–6, subsessile, 3.5–5 mm long, with tips positioned 2–3.5 mm below top of corolla tube; ovary 3–4 mm long; stigmas 2–4 mm long, linear, positioned below anthers. Capsules 4–6 cm long including beak ca. 1 mm long, 7–8 mm diam., with stipes 3–7 mm long, smooth or with ca. 8 longitudinal lines or low ridges; seeds ca. 3 × 1 mm, with filaments ca. 1 cm long. Figure 7E–G.

*Habitat, phenology, and distribution* (Fig. 8). Ecuador to central Peru, in wet forests at 1300–1700 m. Collected in flower in September, in fruit August to October.

This species is distinguished by its relatively small, usually stiff, lanceolate leaf blades with the margins frequently revolute. The flower is described for the first time here.

*Additional specimens examined.* ECUADOR. **Napo:** Cantón Archidona, faldas al S del volcán Sumaco, comunidad El Pacto 9 km al N de la carretera Hollín-Loreto, sector Guagua Sumaco, 00°40'S, 77°35'W, *Zak & Jaramillo 3788* (MO). PERU. **Junín:** Hacienda Schunke above San Ramón, *Schunke A100* (F); Chanchamayo Valley, *Schunke 436* (F).

**3. Hillia subg. Tetrandrae** C. M. Taylor, subg. nov. TYPE: *Hillia tetrandra* Sw.

A subgeneribus ceteris *Hilliae* corollaris hypocrateriformibus 4-lobatis et stigmatibus linearibus infra medium positus differt.

*Calyx* limb lacking or with lobes 4; *corollas* carnose, salverform, white or sometimes pale green on surfaces exposed in bud, lobes 4; *stamens* 4, attached near top of corolla tube; anthers subsessile; *stigmas* linear, positioned below middle of corolla tube.

Five species in the Greater Antilles, Mexico, Central America, and northeastern South America.

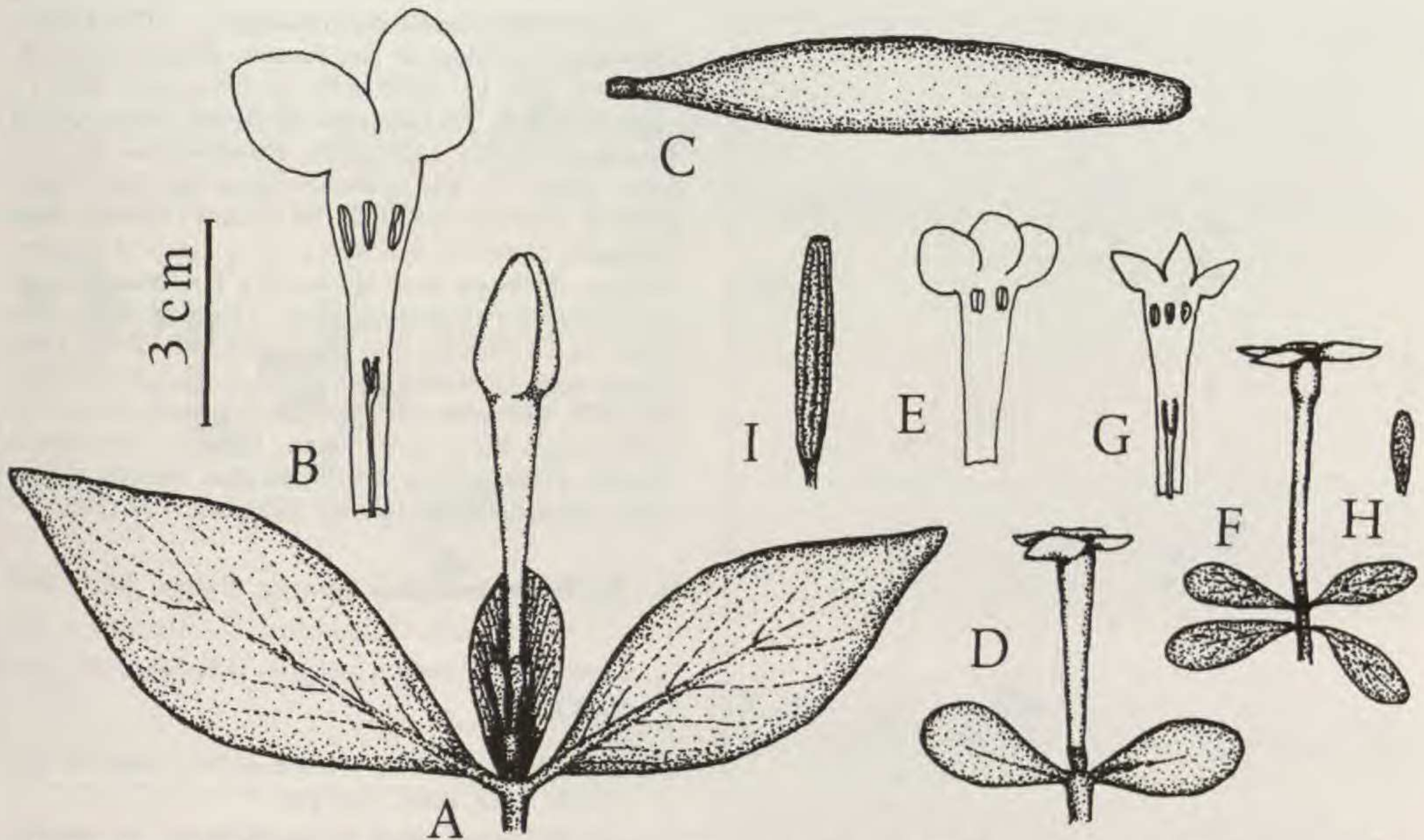


FIGURE 11. A-C. *Hillia loranthoides* Standl.—A. Habit with flower.—B. Flower opened.—C. Capsule. D, E. *Hillia palmana* Standl.—D. Habit with flower.—E. Corolla opened. F-I. *Hillia panamensis* Standl.—F. Habit with flower.—G. Flower opened.—H. Stipule (floral).—I. Capsule. A, from *Breedlove 57488* (F); B, from *Brenes 3839* (F); C, from *Williams 41950* (F); D, E, from *Wilbur 19782* (F); F, G, H, from *Dressler 1487* (NY). A-G to same scale, H to twice this scale.

8. ***Hillia loranthoides*** Standley, *J. Wash. Acad. Sci.* 18: 165. 1928. TYPE: Costa Rica. Guanacaste: Quebrada Serena SE of Tilarán, ca. 700 m, 27 Jan. 1926, *P. C. Standley & J. Valerio 46152* (holotype, US, photo F).

*Hillia macrocarpa* Standl. & Steyerl., *Publ. Field Mus. Nat. Hist., Bot. Ser.* 23: 23. 1943. TYPE: Guatemala. Quezaltenango: lower S-facing slopes of Volcán Santa María between Santa María de Jesús and Calajuache, along great barranca between Finca Pirineos and San Juan Patzulín, 1300–1500 m, 6 Jan. 1940, *J. A. Steyermark 33667* (holotype, F, photo F).

Suffrutescent herbs or shrubs to 1.5 m tall; bark gray-brown, smooth. Leaf blades elliptic to somewhat oblanceolate, 2–10 cm long, 1.6–4.5 cm wide, acute to sometimes acuminate at apex with tip 3–5 mm long, cuneate to attenuate at base, coriaceous and usually thickly so; secondary veins pinnate, 3–5 pairs, plane, without domatia; margins flat; petioles 5–15 mm long; stipules 15–34 mm long, 8–14 mm wide. Flowers solitary; peduncles 1–4 mm long; bracts lacking or 1–3 × 1–2 mm; calyx limb lacking or divided to base, the lobes 4, 5–10 mm long, 1–4 mm wide, ligulate to oblanceolate, acute; corolla salverform, white, the tube 45–75 mm long, the lobes 4, 15–25 mm long, 10–24 mm wide, elliptic, rounded; anthers

4, 7–8 mm long, subsessile, with tips positioned 5–8 mm below top of corolla tube; ovary 3–10 mm long; styles 13–15 mm long; stigmas 8–12 mm long, linear, positioned below middle of corolla tube. Capsules 30–75 mm long including a beak 1–3 mm long, 5–11 mm diam., without stipes, smooth; seeds 1.5–4 × ca. 0.5–1 mm, with filaments 6–13 mm long. Figure 11A–C.

*Habitat, phenology, and distribution* (Fig. 12). Southern Mexico to northern Guatemala and northern to central Costa Rica, in wet forests at 700–2700 m. Collected in flower December to June, in fruit in January, March, and May.

This species differs from *Hillia tetrandra* and *H. maxonii* in its acute or shortly acuminate, usually very thickly coriaceous leaf blades. It may represent an acute-leaved variant of *H. maxonii*. Aside from geographic range, no features separate the plants of Mexico and Guatemala described as *H. macrocarpa* from those of Costa Rica, and this name is placed in synonymy here. The resultant apparently disjunct range of this species is similar to that of *H. panamensis* and some species of *Psychotria* (Hamilton, 1989). The report of *H. triflora* from southern Mexico (Taylor, 1989) was a misidentification of *H. loranthoides*.

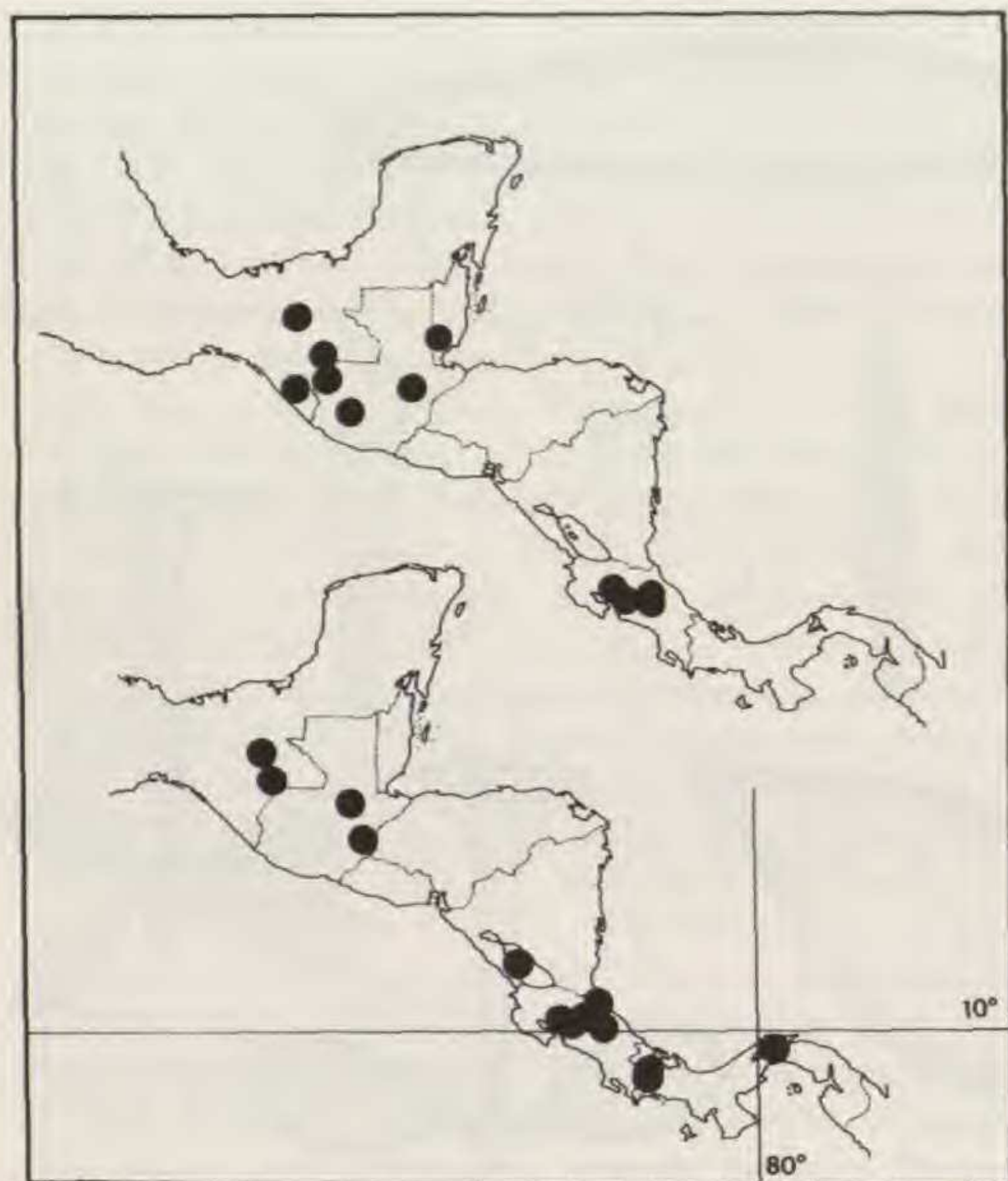


FIGURE 12. Distribution of *Hillia loranthoides* Standl. (upper map) and *H. panamensis* Standl. (lower map) in southern Mexico and Central America.

*Representative specimens examined.* COSTA RICA. **Alajuela:** La Palma de San Ramón, Brenes 3839 (CR, F), 3847 (CR, F), 5439 (CR, F, NY), 6137 (CR, F), Lent 1692 (CR, F). **Cartago:** El Retiro, Santa Cruz de Turrialba, Valerio 1359 (CR). **Puntarenas:** San Luis River valley 1.5 km upstream from San Luis village, Haber & Hammel 1787 (CR, MO). GUATEMALA. **Baja Verapaz:** Sierra de las Minas ca. 5 km S of Purulha, 1600 m, Williams et al. 41950 (F). **Huehuetenango:** km 332 of the Panamerican Hwy. 5 km E of the Mexican border at La Mesilla, Iltis & Lind G202 (WIS). **Quezaltenango:** Quezaltenango, 2666 m, Vaught 305 (US). MEXICO. **Chiapas:** municipio La Trinitaria, 10 km ENE of Dos Lagos above Santa Elena, 1170 m, Breedlove & Almeda 57488 (CAS, NY). **Oaxaca:** vicinity of Concordia, Montecristo, 1100 m, Makrinus 727 (US).

9. *Hillia tetrandra* Swartz, Prodr. 58. 1788.  
TYPE: Jamaica. Coldspring, O. Swartz s.n. (holotype, S not seen; isotype, BM not seen, photo NY).

*Hillia tuxtlensis* Sessé & Mociño ex DC., Prodr. 4: 351. 1830, nom. inval., pro syn.

Suffrutescent herbs or shrubs to 4 m tall; bark gray-brown, smooth. Leaf blades obovate to elliptic, 3–7.5(–10) cm long, 1–3(–4.5) cm wide, obtuse to usually rounded at apex, attenuate at base, subcoriaceous to coriaceous; secondary veins pinnate,

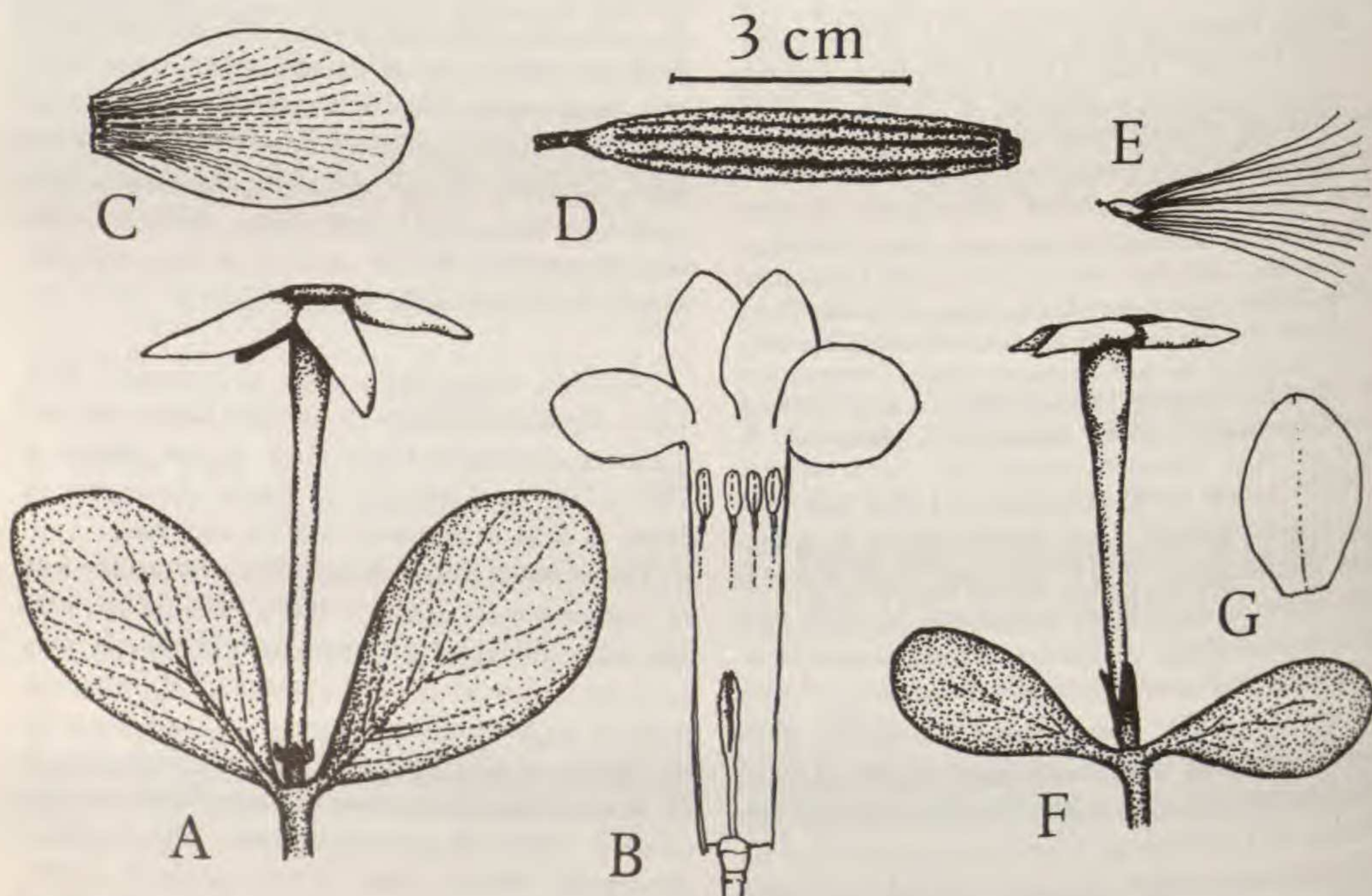


FIGURE 13. A–E. *Hillia tetrandra* Sw.—A. Habit with flower.—B. Flower opened.—C. Stipule (floral).—D. Capsule.—E. Seed. F, G. *Hillia maxonii* Standl.—F. Habit with flower.—G. Stipule (floral). A, B, from Chazaro 3380 (F); C, D, E, from Menéndez L. 85 (F); F, G, from Maxon et al. 7501 (US). A–D, F to same scale, E to three times this scale, G to twice the first scale.



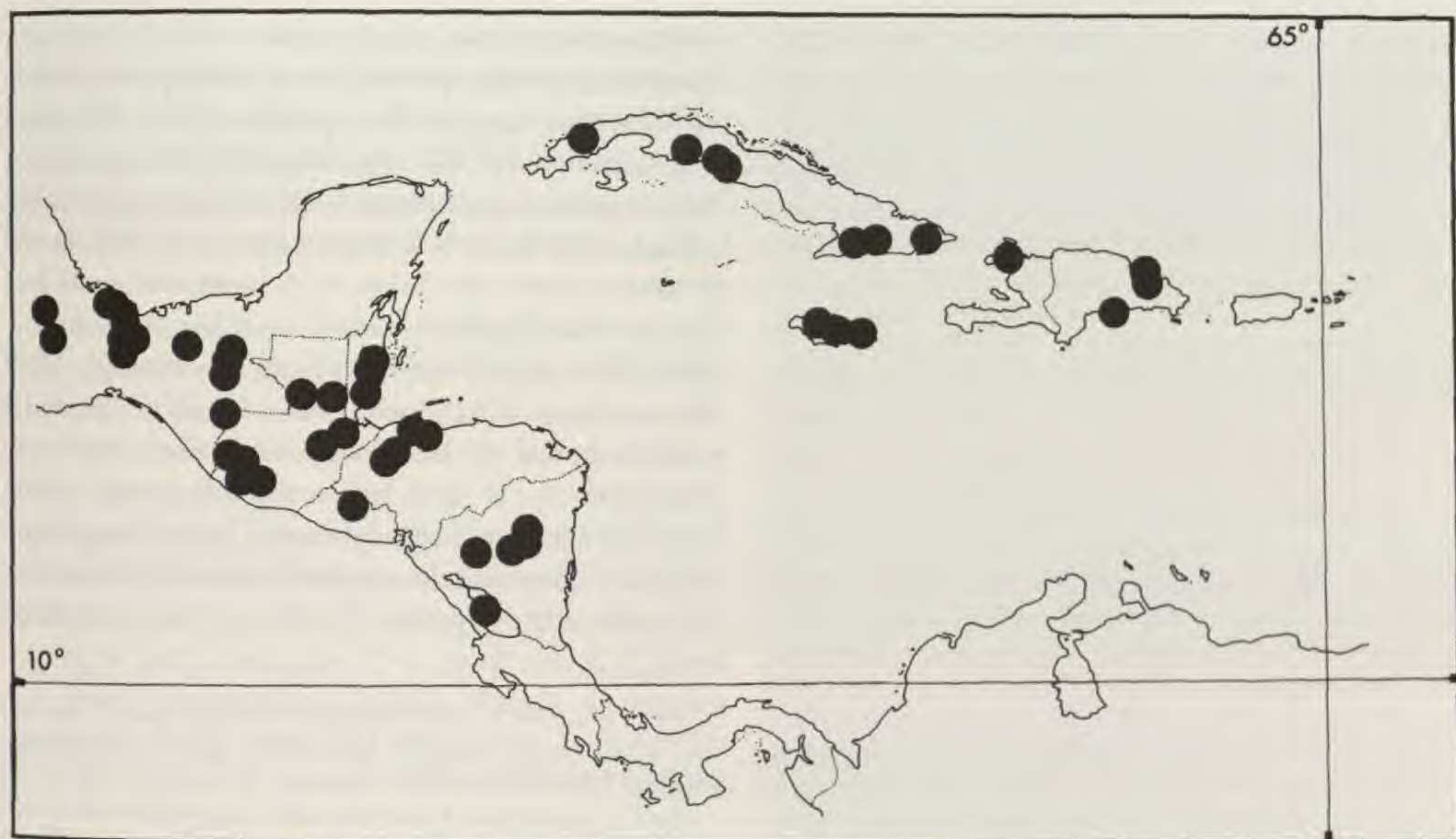


FIGURE 14. Distribution of *Hillia tetrandra* Sw. in southern Mexico, Central America, and the Greater Antilles.

3-5(-6) pairs, plane, without domatia; margins flat; petioles 1-11 mm long; stipules 8-30 mm long, 5-20 mm wide. Flowers solitary; peduncles 1-5(-10) mm long; bracts lacking or 3-4 × 1-2 mm; pedicels 0-3 mm long; calyx limb lacking or divided to base, the lobes 4, 7-19 mm long, often unequal, 1-3(-5) mm wide, oblanceolate to ligulate, rounded; corollas salverform, white, the tube 25-78 mm long, the lobes 4, 10-27 mm long, 8-22 mm wide, elliptic to broadly elliptic, broadly rounded; anthers 4, subsessile, 4.5-5 mm long, with tips positioned 2-3 mm below top of corolla tube; ovary 5-10 mm long; styles 8-18 mm long; stigmas 7-11 mm long, 2-3 mm wide, flattened, linear, positioned below middle of corolla tube. Capsules 25-80 mm long including a beak 1-3 mm long, 5-9 mm diam., not stipitate, with ca. 8 rounded to winged longitudinal ridges to 1 mm high; seeds 2.5-3.5 × 1-1.5 mm, with filaments 8-17 mm long. Figure 13A-E; Standley & Williams (1975: fig. 14).

*Habitat, phenology, and distribution* (Fig. 14). Cuba, Jamaica, Hispaniola, and southern Mexico to northern Nicaragua, in moist to wet, usually rocky forests at 0-1350(-2650) m. Collected in flower March to November, in fruit throughout the year.

This frequently collected species is characterized by its rounded, usually subcoriaceous leaf blades and ridged capsules. Leaf size in plants from Belize and Honduras is frequently markedly larger than

in plants from other areas. Some individual plants from Guatemala, Belize, and Mexico lack a calyx limb; there is no intermediate stage with reduced lobes. This sporadic absence of a calyx limb is found in other *Hillia* species and does not appear to be of taxonomic significance. The corollas vary by as much as 100% in size on material studied, although this may be largely due to shrinkage in dried specimens.

*Hillia tetrandra* is similar to *H. maxonii* of southern Nicaragua to Colombia. The latter can be separated by its smooth to only very slightly ridged capsules and thickly coriaceous leaf blades with the secondary veins usually not discernible. Specimens that lack capsules may be difficult to separate, particularly in Nicaragua where the species occur together. These two species appear to differ ecologically: plants of *H. tetrandra* are generally found below 1000 m in moist formations, while *H. maxonii* is usually reported from very wet forests on ridgetops above 800 m, or from coastal mangrove formations.

*Representative specimens examined.* BELIZE. **El Cayo:** Mt. Pine Ridge, banks of Río On, Lundell 6799 (F, GH, NY, US). **Stann Creek:** Middlesex, Gentle 3006 (MO, NY). **Toledo:** Río Grande, Schipp S-585 (A, F, GH, MO, NY). CUBA. **Cienfuegos:** Buenos Aires, Roig & Acuña 6104 (NY). **Granma:** Pico Turquino, Loma Cordero, Bucher 47 (NY). **Guantánamo:** near Laguna del Galano, Toa, Alain 3856 (GH). **Las Villas:** Trinidad Mountains, near El Naranjo, Webster et al. 209 (A). **Pinar del Río:** Rangel, Rosario Mountains, Alain 6034 (GH, NY). **Santiago de Cuba:** Gran Piedra, Clemente 7144 (GH, US). **Villa Clara:** Las Lagunas, Buenos Aires,

*Jack 6812* (A, DS, F, NY). DOMINICAN REPUBLIC. **El Seibo:** Parque Nacional Los Haitises, entre la caseta #1, Cueva de Arena, y Boca de Infierno, 19°05'N, 69°27'30"W, *Zanoni et al. 35961* (NY). **Samaná:** Samaná Peninsula, Laguna, N of Pan de Azúcar, *Ekman 15099* (GH, US). **San Cristóbal:** near El Cacao, 500 m, *Liogier 17770* (F, NY). EL SALVADOR. **Santa Ana:** Finca Pilón on Cerro de los Naranjos, Volcán Santa Ana, *Williams et al. 15135* (F). GUATEMALA. **Alta Verapaz:** Cubilquitz, *von Tuerckheim 7920* (GH, NY, US). **Izabal:** Río Dulce between Livingston and 6 mi. upriver on N side, *Steyermark 39464* (A, F). **Petén:** La Cumbre, 5 km E on Pusila River bank, *Contreras 8873* (CAS, MO), *8893* (CAS, MO). **Quezaltenango:** Río Samala near Santa María de Jesús, *Standley 84616* (F). **San Marcos:** 6 mi. SW of Tajumulco, NW slopes of Volcán Tajumulco, *Steyermark 36731* (F, NY). **Sololá:** woods bordering Río Bravo in the vicinity of Finca Moca, S-facing slopes of Volcán Atitlán, *Steyermark 479564* (F, US). **Suchitepequez:** S-facing slopes of Volcán Santa Clara 1.5–2 mi. W of Finca El Naranjo, *Steyermark 46808* (F). HAITI. **Nord:** Massif du Nord, sobre Morne Bonnet Levêque, al SO de Milot, 19°6'N, 72°14'W, *Mejía 35780* (NY). HONDURAS. **Atlántida:** Lancetilla Valley near Tela, *Standley 52736* (A, F, US), *54583* (A, F, US), *55581* (A, F, US). **Cortes:** Santa Cruz de Yojoa, *Edwards 654* (A, US). **Santa Bárbara:** near Mochito, *Dickson 1352* (US). JAMAICA. **Cornwall:** Trelawney, Tyre near Troy, *Harris 9448* (F, NY, US). **Middlesex:** St. Catherine, Mt. Diablo, site of Blue Mountain, 2.5 mi. S by road of Hollymount Road, *Hespenheide et al. 1389* (DUKE, GH). **Surrey:** St. Thomas, trail from Bath to Corn Puss Gap, just S of the gap, *Anderson & Sternberg 3311* (DUKE, GH, US). MEXICO. **Chiapas:** mpio. Ocosingo, 5 km SW of Santo Domingo, 120 km SE of Palenque on road to Bonampak, *Davidse et al. 20416* (MO). **Oaxaca:** road between Ixtlán & Valle Nacional, 13 mi. by road above Valle Nacional, 17°40'N, 96°22'W, *Webster & Breckon 15378* (MO). **Tabasco:** mpio. Teapa, Puyacatengo, *Ventura 20644* (F, MO). **Veraacruz:** municipio San Andrés Tuxtla, Los Tuxtlas biological station, 18°34–36'N, 95°04–09'S, *Ibarra 202* (MO), *547* (NY), *1025* (NY), *1983* (MO), *1984* (MO), *Martínez 3075* (F, MO, US). NICARAGUA. **Matagalpa:** Los Tres Laureles, *Neill 7259* (MO). **Rivas:** Isla Ometepe, Volcán Concepción, Altagracia "La Sabana," 11°32'N, 85°35'W, *Robleto 138* (MO). **Zelaya:** Cerro Waylawas, 13°39'N, 84°48–49'W, *Stevens 7404* (MO).

- 10. *Hillia maxonii*** Standley, J. Wash. Acad. Sci. 18: 163. 1928. TYPE: Nicaragua. Managua: Las Nubes and vicinity S of Managua, 800–900 m, 28 June 1928, *W. R. Maxon, A. D. Harvey & A. T. Valentine 7501* (holotype, US, photo F).

*Cosmibuena rhizophorae* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 178. 1940. TYPE: Colombia. Valle: Buenaventura Bay, 0 m, 13 Apr. 1939, *E. P. Killip 34972* (holotype, US, photo F; isotype, F).

Suffrutescent herbs or shrubs to 5(–15) m tall; bark gray-brown, smooth. Leaf blades elliptic to oblanceolate or suborbicular 2.5–10 cm long, 15–35 mm wide, obtuse to rounded at apex, cuneate

to attenuate at base, coriaceous to usually thickly so; secondary veins pinnate, 4–5 pairs, plane, without domatia; margins flat; petioles 3–8(–15) mm long; stipules 12–32 mm long, 8–10 mm wide. Flowers solitary; peduncles 1–2(–4) mm long; bracts lacking or 1–3 × 1–2 mm; calyx limb lacking or divided to base, the lobes 4, 5–6 mm long, 0.5–2 mm wide, ligulate, acute; corollas salverform, white, the tube 42–55 mm long, the lobes 4, 15–27 mm long, 10–17 mm wide, elliptic, rounded; anthers 4, ca. 5 mm long, subsessile, with tips positioned ca. 3 mm below top of corolla tube; ovary 3–10 mm long; style ca. 15 mm long; stigmas ca. 7 mm long, linear, positioned below middle of corolla tube. Capsules 29–60 mm long including beak 1–3 mm long, 5–9 mm diam., not stipitate, smooth to slightly ridged longitudinally; seeds 2–4 × 0.5–1 mm, with filaments 6–13 mm long. Figure 13F, G.

*Habitat, phenology, and distribution* (Fig. 15). Central Nicaragua to Ecuador, in wet forests at 0–2400 m: montane regions, Nicaragua to Panama, to mangrove formations and along rivers, Panama to Ecuador. Collected in flower April, May, July to September, and December, in fruit January to March, May to July, November, and December.

This species is characterized by its coriaceous leaf blades that are obtuse to rounded at the apex and smooth to slightly ridged capsules. Plants from Colombia and Ecuador are apparently disjunct by several hundred miles from those of central Pan-



FIGURE 15. Distribution of *Hillia illustris* (Vell.) K. Schum. (solid circles) and *H. maxonii* Standl. (solid triangles) in Central and South America.

ama and are found in coastal formations rather than wet ridge forests. In Panama plants have been collected in both habitats. No morphological differences between the Central and South American plants are evident. *Cosmibuena macrocarpa* (Benth.) Walp. occupies a similar geographic range and set of habitats.

*Hillia maxonii* is similar to *H. tetrandra*, and these species have sometimes been combined (Dwyer, 1980). The distinctions between them are discussed under the treatment of the latter species. *Hillia maxonii* is also similar to *H. palmana* of southern Central America; this latter species has consistently smaller flowers and usually smaller leaves.

*Representative specimens examined.* COLOMBIA. **Chocó-Valle Border Region:** Alto del Galápago, along Ansermanuevo-San José del Palmar road, 4°40'N, 76°25'W, *Luteyn & Giraldo 12690* (CUVC). **Valle:** Estero del Cangrejal, entre los ríos Yurumanguí y Naya, *Cuatrecasas 16017* (F, US). COSTA RICA. **Alajuela:** La Palma de San Ramón, *Brenes 11900* (F, NY). **Cartago:** near La Sierra ca. 25 km S of Cartago, *Williams et al. 28129* (F). **Guanacaste:** El Silencio near Tilarán, *Standley & Valerio 44733* (US). **Heredia:** Cerros de Zurquí NE of San Isidro, *Standley & Valerio 50691* (US). **Puntarenas:** Monteverde Reserve, *Haber 571* (MO), *1787* (MO), *4501* (MO), *Hammel & Haber 13933* (MO). **San José:** near Finca La Cima above Los Lotes, N of El Copey, *Standley 42599* (US), *42771* (US). ECUADOR. **Carchi:** environs of Chical 12 km below Maldonado on Río San Juan, 1°04'N, 78°17'W, *Madison et al. 4700* (F). NICARAGUA. **Managua:** S of Managua, *Garnier 135* (F). PANAMA. **Bocas del Toro:** near Cerro Colorado ca. 9.4 mi. from Chami camp, 8°35'N, 81°45'W, *McPherson 8941* (MO). **Chiriquí:** distrito Boquete, Fortuna Dam site, *van der Werff & van Hardeveld 6722* (MO). **Coclé:** western slopes and summit of Cerro Valle Chiquito, *Seibert 495* (MO, US). **Panamá:** Cerro Jefe (Cerro Azul), 9°15'N, 79°23'W, *Dwyer & Gauger 7377* (GH, MO), *McPherson 6858* (MO), *7138* (MO), *Mori & Kallunki 6500* (MO, NY). **Veraguas:** 5 mi. W of Santa Fe on road past Escuela Agrícola Alto Piedras, *Croat 23079* (F, MO, NY).

**11. *Hillia palmana*** Standley, J. Wash. Acad. Sci. 18: 164. 1928. TYPE: Costa Rica. Heredia: vicinity of La Palma on road to La Hondura 1500–1700 m, 17–18 July 1923, *W. R. Maxon & A. D. Harvey 8045* (holotype, US).

*Hillia chiapensis* subsp. *grandifolia* Dwyer, Ann. Missouri Bot. Gard. 67: 216. 1980. TYPE: Panama. Veraguas: 6–7 km W of Santa Fe on new road past agriculture school, 2900 ft. [950 m], *M. Nee 9698* (holotype, MO).

Suffrutescent herbs or shrubs to 5 m tall; bark gray-brown, smooth. Leaf blades elliptic to oblanceolate, 2–7 cm long, 1.5–3.5 cm wide, obtuse to

rounded or rarely truncate at apex, cuneate to attenuate at base, coriaceous; secondary veins pinnate, 3–4 pairs, plane, without domatia; margins flat; petioles 3–8 mm long; stipules 12–20 mm long, 8–10 mm wide. Flowers solitary; peduncles 1–2 mm long; bracts lacking or 1–3 × 1–2 mm; calyx limb lacking or divided to base, the lobes 4, 4–6 mm long, 1–2 mm wide, ligulate, acute to rounded; corollas salverform, white, the tube 35–40 mm long, the lobes 4, 8–12 mm long, 6–12 mm wide, elliptic to suborbicular, rounded; anthers 4, ca. 5 mm long, subsessile, with tips positioned 2–3 mm below top of corolla tube; ovary 3–5 mm long; style ca. 15 mm long; stigmas ca. 7 mm long, linear, positioned below middle of corolla tube. Capsules 3–6 cm long including beak 1–3 mm long, 5–8 mm diam., not stipitate, smooth; seeds 2–4 × 0.5–1 mm, with filaments 6–13 mm long. Figure 11D, E.

*Habitat, phenology, and distribution* (Fig. 16). Central Nicaragua to central Panama, in wet forests at 675–2500 m. Collected in flower December to October, most frequently May to June, in fruit December to February, May, and July to October.

This species is distinguished by its medium-sized leaf blades that are usually obtuse to rounded at the apex and small flowers. It is similar to *Hillia maxonii* and *H. panamensis*; the distinctions among these three species are discussed in the treatments of the last two species.

*Representative specimens examined.* COSTA RICA. **Alajuela:** Fila Volcán Viejo, San Carlos, *Gómez-Laurito 11095* (CR). **Cartago:** Volcán Irazú, SW slopes near Guayabillos, *Cufodontis 465* (F). **Guanacaste:** entre la laguna del Arenal y el Alto de La Carpintera, cerca de Tilarán, *Brenes 12644* (F, NY). **Heredia:** entre Finca La Georgina y Vara Blanca, *Jiménez 2075* (CR, F, NY). **Limón:** Reserva Indígena Talamanca, camino a Soki entre la quebrada Amubri, margen izquierda del río Lari, 9°29'40"N, 82°03'40"W, 200 m, *Chacón 18* (MO). **Puntarenas:** Monteverde area, 10°20'N, 84°50'W, *W. Haber 760* (MO), *1156* (MO), *4564* (MO), *6174* (MO), *Haber & Bello 3671* (CR, MO), *4263* (CAS, CR, MO), *4267* (CR, MO), *4530* (MO). **San José:** near Altos de Tablazo ca. 7 km SSE of Higuito, ca. 9 km SSE of Desemparados, *Wilbur 19782* (CAS, CR, F, MO, NY, US). NICARAGUA. **Boaco:** 2 km al N de San José de los Remates, 12°36'N, 85°45'W, *Moreno 24904* (MO), *24936* (MO). **Granada:** lado NO del volcán Mombacho, Finca San Joaquín, 11°50'N, 85°59'W, *Moreno & Henrick 8510* (MO). **Jinotega:** ca. 1.5 km from Hwy. 3 on road to Aranjuez, 13°02'N, 85°55'W, *Stevens 5947* (MO). **Matagalpa:** ridge along road between La Danta and La Luna, 12°40'N, 85°43'W, *Stevens 9616* (MO). PANAMA. **Bocas del Toro:** trail from Boquete to Cerro Pate Macho, 8°49'N, 82°24'W, *McPherson & Merello 8328* (MO). **Chiriquí:** vicinity of Fortuna Dam, 8°40'N, 79°50'W, *McPherson 10577* (MO). **Darién:** E slope of

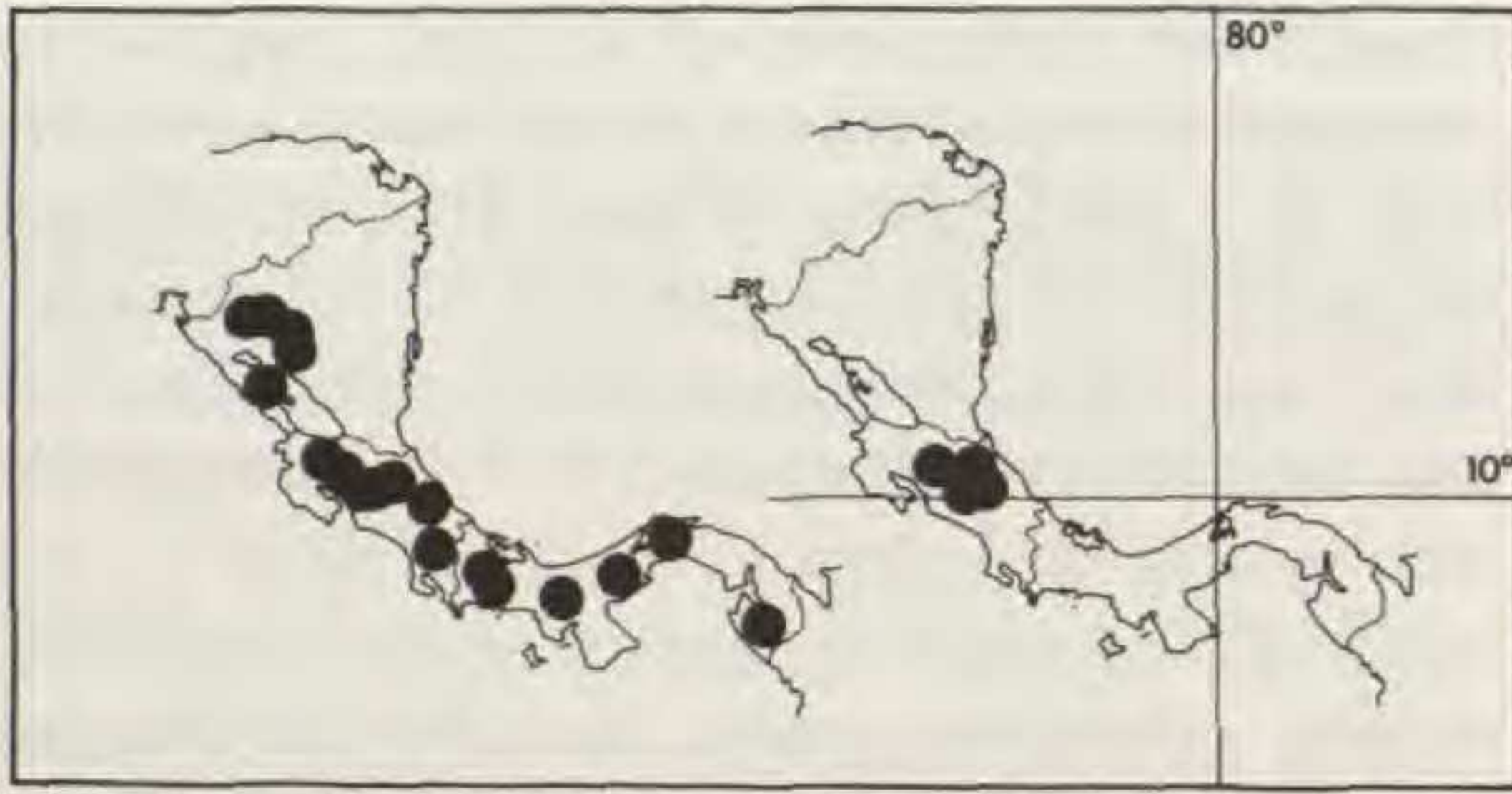


FIGURE 16. Distribution of *Hillia palmana* Standl. (left-hand map) and *H. grayumii* C. M. Taylor (right-hand map) in Central America.

Cerro Sapo, Hammel 1284 (MO). **Panamá:** E slope of Cerro Jefe (Cerro Azul), Tyson 3436 (GH, MO). **Vera-guas:** Cerro Tute, 8°32'N, 81°07'W, Knapp & Dressler 5398 (MO), Mori et al. 7559 (MO).

**12. *Hillia panamensis*** Standley, N. Amer. Fl. 32(2): 117. 1921. TYPE: Panama. Chiriquí: Cerro de la Horqueta around Los Siguan Camp, 1700 m, 17–19 Mar. 1911, H. Pittier 3190 (holotype, US; isotype, US).

*Hillia chiapensis* Standl., J. Wash. Acad. Sci. 16: 16. 1926. TYPE: Mexico. Chiapas: near Fénix, Apr. 1925, C. A. Purpus 262 (holotype, US, photo F).

*Hillia hathewayi* Fosberg, Sida 2: 387. 1966. TYPE: Costa Rica. Heredia: S slope of Volcán Barba, 1950 m, 26 May 1965, W. H. Hatheway 1371 (holotype, US; isotypes, F, GH).

Suffrutescent herbs or shrubs to 4 m tall; bark gray-brown, smooth. Leaf blades elliptic to narrowly elliptic, 6–15 mm long, 3–10 mm wide, rounded to obtuse at apex, cuneate to attenuate at base, subcoriaceous to coriaceous; secondary veins pinnate, ca. 2 pairs, smooth, without domatia; margins flat; petioles 1–2 mm long; stipules 4–5 mm long, 1–1.5 mm wide. Flowers solitary; peduncles ca. 1 mm long; bracts lacking; calyx limb usually lacking or divided to base, the lobes 4, 6–7 mm long, 1–3 mm wide, ligulate, rounded; corollas white, salverform, the tube 24–35 mm long, the lobes 4, 8–10 mm long, 3–5 mm wide, lanceolate, acute; anthers 4, 1–2 mm long, subsessile, with tips positioned 1–2 mm below top of corolla tube; ovary 2–3 mm long; style 7–12 mm long; stigmas 5–10 mm long, linear, positioned below middle of corolla tube. Capsules 2–4 cm long including beak 1–2 mm long, ca. 3 mm diam., not stipitate, smooth or usually with ca. 10 longitudinal ridges; seeds 1–2 × 0.5 mm, with filaments 6–13 mm long. Figure 11F–I; Dwyer (1980: fig. 48, as *Hillia chiriquiensis*).

*Habitat, phenology, and distribution* (Fig. 12). Southern Mexico to Guatemala and Belize,

and southern Nicaragua to western Panama, in wet forests at 20–2300 m. Collected in flower December, January, and June through August, in fruit November to April, August, and September.

This species is distinguished by its lanceolate acute corolla lobes and relatively small, usually narrow leaf blades, stipules, and capsules. The plants of southern Mexico and Guatemala are apparently disjunct from those of southern Central America, but no morphological differences are apparent and they appear to occupy similar habitats. Therefore *Hillia chiapensis* is here placed in synonymy. Similar apparently disjunct geographic ranges are seen in *H. loranthoides* and species of *Psychotria* (Hamilton, 1989).

*Hillia panamensis* is similar to *H. palmana*; the latter species has elliptic rounded corolla lobes 6–12 mm wide, and usually larger, proportionally broader leaf blades, stipules, and capsules.

Several sterile and fruiting specimens from relatively low elevations in Nicaragua and Costa Rica are provisionally included here, although they have relatively broad leaves and ridged capsules.

*Representative specimens examined.* BELIZE. **Toledo:** Maya Mountains, Holst 4292 (MO). COSTA RICA. **Alajuela:** Cantón Alfaró Ruiz, Palmira, Smith 2737 (F). **Cartago:** Turrialba, Instituto Interamericano de Ciencias Agrícolas, León 2999 (CR). **Guanacaste:** El Dos de Tilarán, 13 km NW of Monteverde, 10°25'N, 84°55'W, 900 m, Haber et al. 5273 (MO). **Limón:** Cerro Coronel, E of Laguna Danto, 10°41'N, 83°38'W, Stevens 23919 (CR), Stevens & Montiel 24389 (CR, MO). **Puntarenas:** Monteverde area, Haber 384 (MO), 562 (MO). GUA-TEMALA. **Alta Verapaz:** between Finca Chimote near Rubeltien and Finca Cubilgüitz, Steyermark 44195 (F, US). **Chiquimula:** Cerro Tixixí 3–5 mi. N of Jicotán, Steyermark 31627 (F, NY). MEXICO. **Chiapas:** municipio de Ocosingo, near Laguna Ocotol Grande ca. 25–30 km SE of Monte Líbano, ca. 45 km E of Ocosingo, Dressler 1487 (NY, US). NICARAGUA. **Rivas:** Isla de Ometepe, Volcán Maderas, 11°26–37'N, 85°30–33'W, Moreno 18806 (MO), 19689 (MO), 19852 (MO), Stevens 6552 (MO). PANAMA. **Bocas del Toro–Chiriquí Border:** Cerro Colorado, 8 km from intersection of the ridge road on the road to Escopeta, Folsom 4785 (MO). **Panamá:** Cerro Jefe, Hayden 1021 (MO).

**4. *Hillia* subg. *Illustres*** C. M. Taylor, subgenov. TYPE: *Hillia illustris* (Vell.) K. Schum.

A subgeneribus ceteris *Hilliae* corollis infundibularibus 5–9-lobatis viridibus flavovirentibus vel colore atropurpureo suffusis et stigmatibus subcapitatis supra antheras positus differt.

*Calyx* limb lacking, very reduced, or with 5–9 well-developed lobes; *corollas* membranaceous to carnose, funnellform, green to yellow-green or flushed with dull dark purple, the lobes 5–9, triangular to suborbicular; *stamens* attached above middle or near top of corolla tube, the anthers

subsessile or with filaments well developed; *stigmas* subcapitate, positioned above anthers; *capsules* usually stipitate.

Seven species throughout northern and central South America, one extending north to Costa Rica.

13. *Hillia grayumii* C. M. Taylor, Selbyana 12: 137. 1991. TYPE: Costa Rica. Heredia: Finca La Selva, the OTS field station near Puerto Viejo de Sarapiquí, near the junction of the Ríos Puerto Viejo and Sarapiquí, 100 m, 5 May 1980, M. H. Grayum 2793 (holotype, DUKE; isotype, DUKE).

Shrubs to 1 m tall, or lianas; bark gray-brown, smooth. Leaf blades elliptic, 9–16 cm long, 1.5–6.5 cm wide, acuminate at apex with tip 1–2 cm long, acute at base, coriaceous; secondary veins pinnate, 3–6 pairs, plane, without domatia; margins flat; petioles 3–20 mm long; stipules ca. 4 cm long, 6–8 mm wide. Flowers solitary; peduncles 2–3 mm long; bracts 1–2 mm long; pedicels 2–3(–5) mm long; calyx limb ca. 0.5 mm long, truncate to dentate; corolla broadly funnelform, bright pale green to yellow-green, the tube 43–50 mm long, the lobes 6, 8–9 mm long, triangular, obtuse to rounded; stamens 6, the filaments ca. 10 mm long, the anthers ca. 9 mm long, with tips positioned 3–5 mm below top of corolla tube; ovary 7–8 mm long; stigmas ca. 3 mm long, subcapitate, positioned immediately above anthers. Capsules ca. 12 cm long, ca. 12 mm diam., not stipitate, smooth or with 8–10 low longitudinal ridges; seeds ca. 3 × 0.5 mm, with filaments 15–16 mm long. Taylor et al. (1991: fig. 3).

*Habitat, phenology, and distribution* (Fig. 16). Costa Rica, in wet forest at 0–200 m. Collected in flower May and June, in fruit March.

This species is distinguished by its reduced calyx limb and bright pale green to yellow-green, broadly funnelform corollas. It is similar to *Hillia illustris* and *H. psammophila* of South America; the distinctions among these are discussed in the treatments of the other two species. Vegetatively *H. grayumii* resembles *H. triflora* var. *triflora*, with which it is sympatric, and these species can be difficult to separate in fruit.

*Hillia grayumii* appears to be uncommon and ephemeral. It was first discovered in a well-studied area of the La Selva Biological Station, where it apparently grew to flowering size rapidly, but within two years was no longer found in the vicinity (Hammel, pers. comm.; Grayum, pers. comm.).

*Representative specimens examined.* COSTA RICA. **Alajuela:** Monteverde Biological Reserve, Río Peñas

Blancas, 10°19'N, 84°43'W, Haber & Cruz 8464 (CR). **Cartago:** on Casa de Tajas ridge above Río Gato, 9°47'N, 83°41'W, Lent 3703 (F, NY). **Limón:** shores of Caño Pereira, 10°45–47'N, 83°36–37'W, Stevens et al. 25120 (CR, MO).

14. *Hillia psammophila* Steyermark, Mem. New York Bot. Gard. 19(5): 211. 1963. TYPE: Venezuela. Bolívar: vecinidad del Camp 125 en el Km 125, entre Luepa y Cerro Venamo, vecinidad de Cerro Uei, 1100 m, 20 Apr. 1960, J. Steyermark & S. Nilsson 392 (holotype, VEN).

Suffrutescent vines, climbing by adventitious roots; bark smooth. Leaf blades elliptic to lance-elliptic, 4.5–6.5 cm long, 2–3 cm wide, acuminate at apex with tip 4–10 mm long, acute at base, coriaceous; secondary veins pinnate, 3–4 pairs, plane, without domatia; margins flat; petioles 6–11 mm long; stipules not seen. Flowers solitary; peduncles 4–5 mm long; bracts not seen; calyx limb divided to base, the lobes 6, ca. 18 mm long, 3–3.5 mm wide, triangular to narrowly elliptic, rounded; corollas funnelform, yellow-green, the tube ca. 6 cm long, the lobes 6, ca. 1 cm long, ca. 15 mm wide, rounded; anthers 6, sessile, 7–8 mm long, with tips positioned ca. 5 mm below top of corolla tube; ovary ca. 7 mm long; stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules not seen. Steyermark (1963: fig. 74).

*Habitat, phenology, and distribution* (Fig. 8). South-central Venezuela, in wet forests at 1100 m. Collected in flower in April.

This species is distinguished by its relatively small leaves and anthers situated just below the top of the corolla tube. The original and subsequent descriptions of this species (Steyermark, 1963, 1974) describe the filaments as ca. 15 mm long, but the anthers are sessile and the filaments adnate to the corolla for ca. 45 mm. *Hillia psammophila* is similar to *H. illustris*; the distinctions between them are discussed in the treatment of the latter species. *Hillia psammophila* is also similar to *H. grayumii* of Costa Rica and may be closely related; *H. grayumii* differs in its larger leaf blades, 9–16 cm long, and its anthers positioned just below the top of the corolla tube.

15. *Hillia illustris* (Vellozo) K. Schumann in Martius, Fl. Bras. 6(6): 202. 1889. *Saldanha illustris* Vell., Fl. Flum. 3: 141, t. 157. 1825. TYPE: Brazil. Rio de Janeiro area, Vell., Fl. Flum. t. 157, 1825, lectotype designated by Taylor (1993).

*Hillia tubaeiflora* Cham., Linnaea 9: 260. 1834. TYPE:

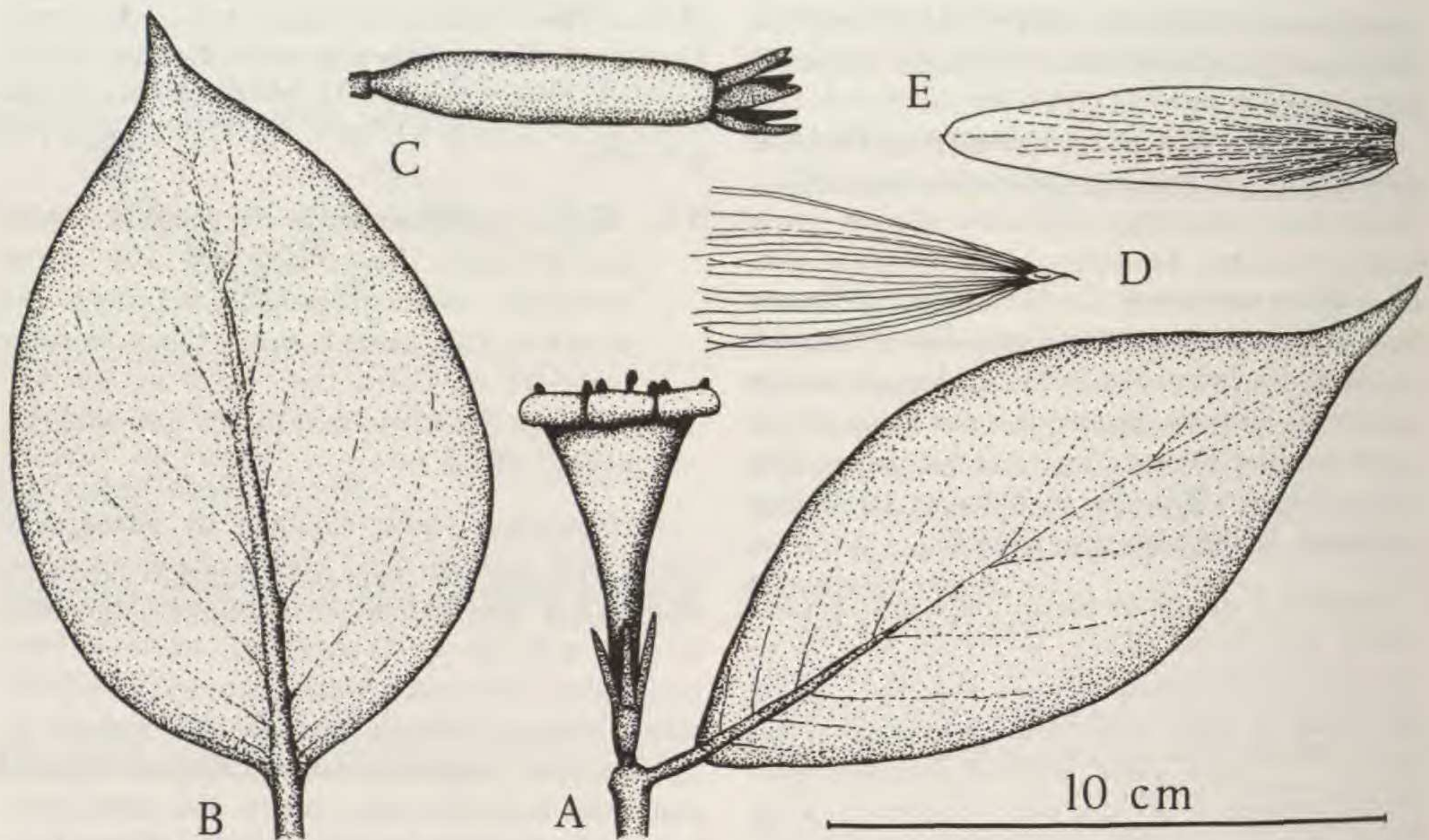


FIGURE 17. A-E. *Hillia illustris* (Vell.) K. Schum.—A. Habit with flower.—B. Leaf.—C. Capsule.—D. Seed.—E. Stipule (floral). A, E, from *Dusén 15539* (MO); B, from *Vásquez & Jaramillo 4130* (MO); C, D, from *Encarnación 26178* (MO). A-C to same scale, D to three times this scale, E to twice the first scale.

Brazil. *Brazilia aequinoctialis*, *Sello 5988* (holotype, B destroyed, photos F, GH, NY; isotype, F).

*Hillia trinitensis* R. O. Williams & Cheeseman, *Fl. Trinidad & Tobago* 2: 7. 1928. TYPE: Trinidad. Taruaria Forest, 16 Feb. 1915, *W. E. Broadway 7807* (lectotype, designated by Steyermark (1972: 288), NY; isotype, TRIN not seen).

*Hillia goudotii* Standl., *Publ. Field Columbian Mus., Bot. Ser.* 8: 338. 1931. TYPE: Colombia. Valle: Río Sucio, Jan. 1844, *J. Goudot s.n.* (holotype, P, photo F; isotype, F).

Suffrutescent herbs, shrubs, or small trees to 8 m tall; bark gray-brown to red-brown, smooth, sometimes peeling. Leaf blades elliptic, 8.5–15 cm long, 3–8 cm wide, acute to usually acuminate at apex with tip 5–10(–15) mm long, acute to cuneate at base, thickly coriaceous; secondary veins pinnate, 4–7 pairs, plane or with midrib sometimes prominulous abaxially, without domatia; margins flat; petioles 6–13 mm long; stipules subtending leaves 23–33 mm long, 7–10 mm wide, those subtending flowers 26–60 mm long, 6–18 mm wide. Flowers solitary(–3); peduncles 1–5 mm long; bracts not seen; calyx limb divided to base, the lobes 6, 9–35 mm long, often unequal by ca. 1 mm, 1.5–2(–4) mm wide, narrowly triangular, acute; corolla funnellform to broadly so, bright green to yellow-green, the tube 48–61 mm long, the lobes 6, 8–16 mm long, elliptic, obtuse to rounded; anthers 6, sessile, 10–11 mm long, with tips positioned at or 1–2 mm above top of corolla tube;

ovary 6–10 mm long with stipe 1–5 mm long; stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules with peduncles 2–10 mm long, (50–)85–115 mm long including beak 1–5 mm long, 8–15 mm diam., stipe 5–10 mm long, smooth or usually with ca. 10 low longitudinal ridges; seeds 2–4 × 0.5–2 mm, with filaments 14–22 mm long. Figure 17; Robbrecht (1988: fig. 6b, as *Hillia tubiflora*).

*Habitat, phenology, and distribution* (Fig. 15). Sporadic throughout tropical South America, in wet forests at 70–800 m, frequently along rivers. Collected in flower December, January, May to July, and September, in fruit January to March and May to November.

This species is distinguished by its relatively large, acute to acuminate leaf blades with pinnate venation and stipitate capsules. Both vegetative and reproductive parts vary rather widely in size, as in several other species of *Hillia*.

*Hillia illustris* is similar to *H. ulei*; the latter species is distinguished by its usually shorter, proportionally broader leaf blades with subpalmate venation. *Hillia illustris* also resembles *H. grayumii*, which has capsules that are not stipitate, a very reduced calyx limb, and filaments ca. 10 mm long, and *H. psammophila*, which has smaller leaf blades, filaments ca. 15 mm long, and anthers positioned below the top of the corolla tube.

There appears to be no morphological difference between plants of Trinidad and the mainland, and *Hillia trinitensis* is not maintained here. *Hillia goudotii*, based on a single specimen, differs from typical *H. illustris* only in having flowers borne in a cyme of three rather than solitary. A similar variation in flower number is seen in *H. saldanhae*, and the reverse variation, with flowers usually three but rarely one or two, is found in *H. triflora*. Therefore *Hillia goudotii* is not maintained here. Some authors (e.g., Robbrecht, 1988) have corrected the spelling of *H. tubaeflora* (tuba-shaped) to "tubiflora" (tube-shaped), but Chamisso based his description on a flowering specimen, and most likely intended to apply the first, more appropriate epithet.

*Representative specimens examined.* BOLIVIA.

**Beni:** provincia Balliva, lower slopes of Serranía Pilón Lajas, 14.3 km N of bridge over Río Quiquibey, 15°19'S, 67°03'W, *Solomon* 13957 (MO). **La Paz:** provincia Yungas Sur, basin of Río Bopi, Asunta near Evenay, *Krukoff* 10697 (A, F, MO, NY). BRAZIL. **Amapá:** região de Río Jarí Monte Dourado, Planalto Amazônia, *Silva* 927 (NY). **Paraná:** Tacarehy, *Dusén* 15539 (F, GH, MO). **São Paulo:** Sete Varras, S entrance to Carlos Botelho State Park, 24°22'S, 46°55'W, *Gentry et al.* 59053 (MO). COLOMBIA. **Amazonas-Vaupés Border:** río Apaporis, entre el río Pacoa y el río Kananari, Soratama, *Schultes & Cabrera* 13030 (F, NY). **Chocó-El Valle Border Region:** carretera Ansermanuevo-San José de Palmar, Alto de Galápago, *Forero et al.* 2868 (COL). **Vaupés:** Mitú and vicinity, island in Río Vaupés just below Urania, *Zarucchi et al.* 1885 (COL, F, GH). ECUADOR. **Morona-Santiago:** Misión Bomboiza, 3°29'S, 78°34'W, *Holm-Nielsen & Jeppesen* 4202 (AAU). **Napo:** cantón Tena, 10 km O de la estación biológica Jatún Sacha, carretera hacia Tena, 1°03'S, 77°40'W, *Palacios & Iguago* 4433 (MO). FRENCH GUIANA. **Cayenne:** region de la Haute Armontabo (Bas Oyapock), *de Granville* 4362 (COL, P). **Saint Laurent de Maroni:** Rivière Mana, Crique Arouany, *F. Hallé* 622 (P). PERU. **Cuzco:** provincia La Convención, Camp Zero ca. 1 hour walk up Río Mapitunuari from Río Apurimac, Luisiana, *Dudley* 11426 (F). **Huánuco:** provincia Leoncio Prado, distrito Rupa Rupa, al E de Tingo Maria, cerca al cerro Quemado, *Schunke* 10292 (F, MO, NY). **Loreto:** provincia Maynas, distrito Alto Nanay, along trail to Santa Rosa, Santa María de Nanay, *Simpson & Schunke* 806 (COL, F, MO, NY). SURINAM. **Brokopondo:** 2 km S of Affobakka along Sara Creek, Afterwards Lake, *van Donselaar* 2109 (NY). **Marowijne:** ab Moengotapoe ad Grote Zwiebelwamp, *Lanjouw & Lindeman* 628 (NY). **Nickerie:** Wilhelmina Gebegte, Zuid River 2 km above confluence with Lucie River, 3°10'-20'N, 56°29'-49'W, *Irwin et al.* 55870 (COL, MO, NY). VENEZUELA. **Anzoátegui:** along Río León NE of Bergantín, *Steyermark* 61433 (F). **Bolívar:** summit of W-facing escarpment E of Miamo, Hato de Nuria, Altiplanicie de Nuria, *Steyermark* 88835 (NY). **Delta Amacuro:** departamento Antonio Díaz, Caño Guinquina, *Marciano et al.* 70-2-77 (MO).

**16. *Hillia ulei*** K. Krause, *Verh. Bot. Vereins Prov. Brandenburg* 50: 97. 1908; K. Schum. ex Ule, in H. Karst. & Schenck, *Vegetationsbilder* 2, sub tab. 1-2: 3. 1904, nom. nud. TYPE: Peru. Loreto: prope Yurimaguas, Aug. 1902, *E. Ule* 6305 (holotype, B destroyed, photos F, GH, MO, NY; isotype, F). Steyermark (1972) cited *Ule* 6303 as the type collection, but this seems to be an error.

*Hillia viridiflora* Kuhl. & Silveira, *Arch. Jard. Bot. Rio de Janeiro* 4: 370, t. 34. 1925. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro Botanical Garden, Apr. 1920, *Ule* RB-15737 (holotype, RB not seen; isotype, B destroyed, photos F, MO, NY, US).

*Hillia irwinii* Steyermark, *Mem. New York Bot. Gard.* 23: 287. 1972. TYPE: Brazil. Amapá: Río Jarí near Cachoeira Macacoara, 0°53'N, 53°21'W, 200 m, 26 Aug. 1961, *H. S. Irwin & W. A. Egler* 46683 (holotype, NY; isotypes, F, GH, NY, US).

*Hillia schultesii* Steyermark, *Mem. New York Bot. Gard.* 23: 287. 1972. TYPE: Colombia. Amazonas-Vaupés border: río Apaporis, entre el río Pacoa y el río Kananari, boca del Pacoa, 250 m, 18 July 1951, *R. E. Schultes & Cabrera* 13075 (holotype, US, photo NY).

Suffrutescent herbs or shrubs to 2 m tall; bark gray-brown, smooth. Leaf blades elliptic to broadly elliptic, 2-6.5(-7.5) cm long, 1.3-4 cm wide, acute to usually acuminate at apex with tip 3-5 mm long, rounded to cuneate at base, thickly coriaceous; secondary veins subpalmate, 5-7 pairs, plane or with midrib sometimes prominulous abaxially, without domatia; margins flat; petioles 4-11 mm long; stipules 5-17 mm long, 1.5-8 mm wide. Flowers solitary; peduncles 1.5-2 mm long; bracts lacking or 2-3 × 0.5-1.5 mm; calyx limb divided to base, the lobes 7-10, 8-15 mm long, often unequal by 1-3 mm, 1-2 mm wide, narrowly ligulate to triangular, acute to rounded; corollas broadly funnellform, bright green to yellow-green, the tube 28-39 mm long, lobes 7-10, 6-7 mm long, rounded; anthers 8, subsessile, 6-8 mm long, with tips positioned at top of corolla tube; ovary 5-10 mm long, stipes 8-10 mm long; stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules with peduncles 1.5-3 mm long, 6-10.2 cm long including beak 1-5 mm long, 8-10 mm diam., stipes 8-15 mm long, smooth; seeds 1-2 × 0.5-1 mm, with filaments 11-24 mm long. Figure 18.

*Habitat, phenology, and distribution* (Fig. 6). Sporadic throughout tropical South America and eastern Panama, in wet forests at 0-900 m, most frequently along rivers. Collected in flower March to May, July, and August, in fruit January, March to May, July to September, and November.

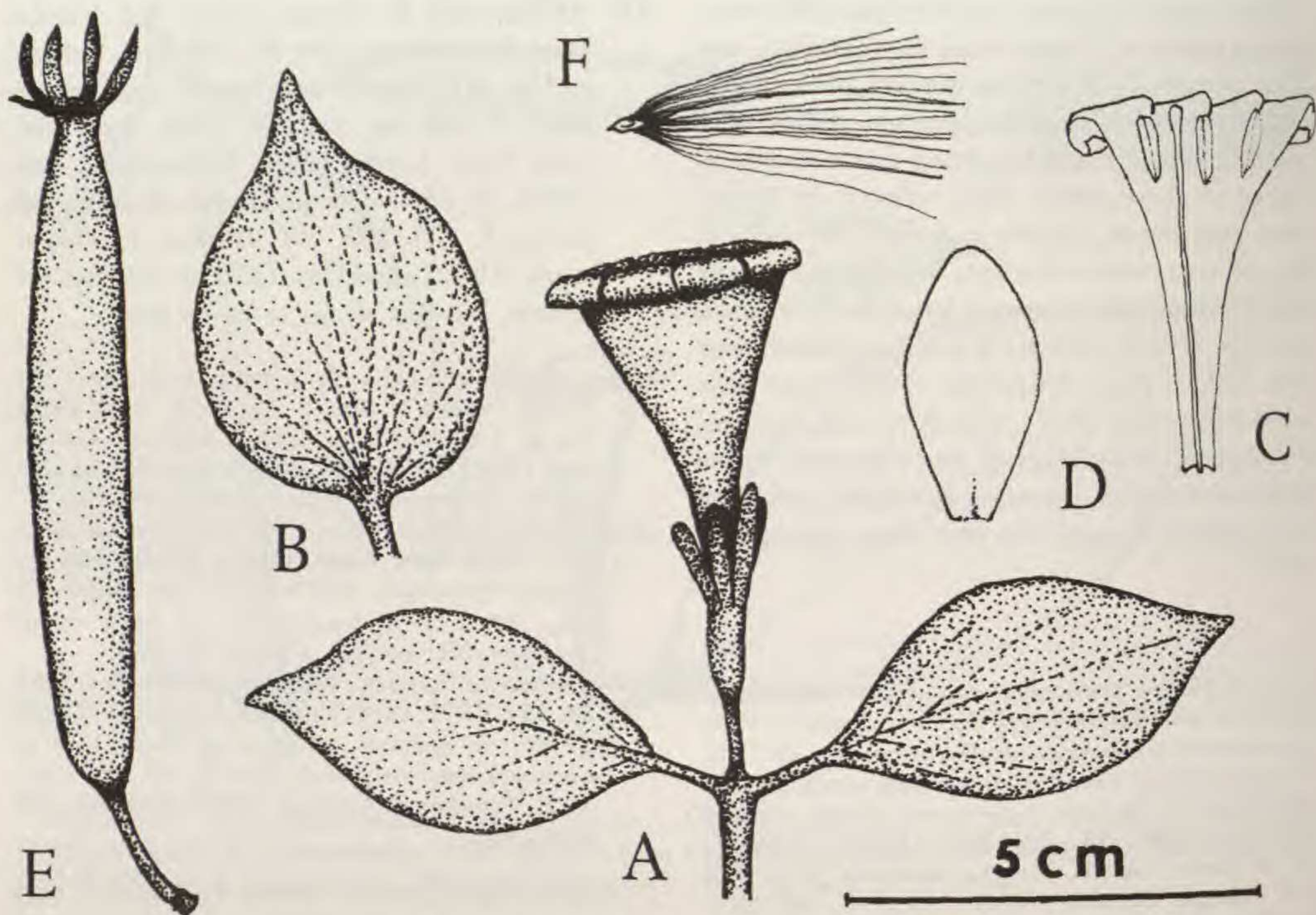


FIGURE 18. A-F. *Hillia ulei* K. Krause.—A. Habit with flower.—B. Leaf.—C. Flower opened.—D. Stipule (floral).—E. Capsule.—F. Seed. A, D, E, F, from *McDaniel & Rimachi 25763* (F); B, from *Schunke V. 4784* (F); D, from *Schultes 13075* (US). A-C, E to same scale; D, F to twice this scale.

This species is distinguished by its subpalmate leaf venation, otherwise in *Hillia* found only in *H. oaxacana* (subg. *Ravnia*) of Mexico. The green flowers usually become dark brown or black when dried. Size of both vegetative and reproductive structures varies, as does relative broadness of the leaf blades, stipules, calyx lobes, and corolla lobes. This variation is continuous, and shows no geographic pattern. Consequently several species recognized by Steyermark (1972) based only on wide geographic separation and differences in sizes of parts are not recognized here.

Steyermark separated *Hillia viridiflora* based on its corolla size, 3–3.5 cm long by 12 mm wide at the tube top in contrast to 4 cm long by 22 mm wide in *H. ulei*, and its “oblong-lanceolate” acute corolla lobes 5 mm wide, in contrast to lobes suborbicular, rounded, and 7 mm wide in *H. ulei*. Based on these criteria, *H. viridiflora* is represented by a single collection. However, collections included by Steyermark in *H. ulei* encompass the measurements of *H. viridiflora* in their range of corolla size and shape; additionally, the one flower available to characterize *H. viridiflora* appears to be immature, and thus probably not fully expanded

in either the tube or the throat. The geographic disjunction between the type locality for *H. ulei* and the general range of this species further north no doubt influenced Steyermark’s taxonomy. However, Ule brought many living collections from the Amazon basin to propagate in the Rio de Janeiro Botanical Garden, and Kuhlmann and Silveira stated in their species description that the plant appeared rather mysteriously, flowered, and disappeared from the Botanical Garden and was not seen elsewhere.

Steyermark separated *Hillia irwinii* based on its ten calyx lobes and corollas ca. 5 cm long with emarginate lobes, in contrast to calyx lobes five to eight and corollas 3–4.5 cm long with triangular lobes in his circumscription of *H. ulei*. Based on these criteria, *H. irwinii* is represented by two collections. However, by my measurement the corolla of the type collection is 43 mm long, and the corolla lobes of this specimen are rounded rather than emarginate. The type collection of *H. irwinii* has ten calyx and corolla lobes and the paratype collection has nine, in contrast to seven to eight calyx and corolla lobes in other specimens of *H. ulei*. However, calyx and corolla lobe number vary



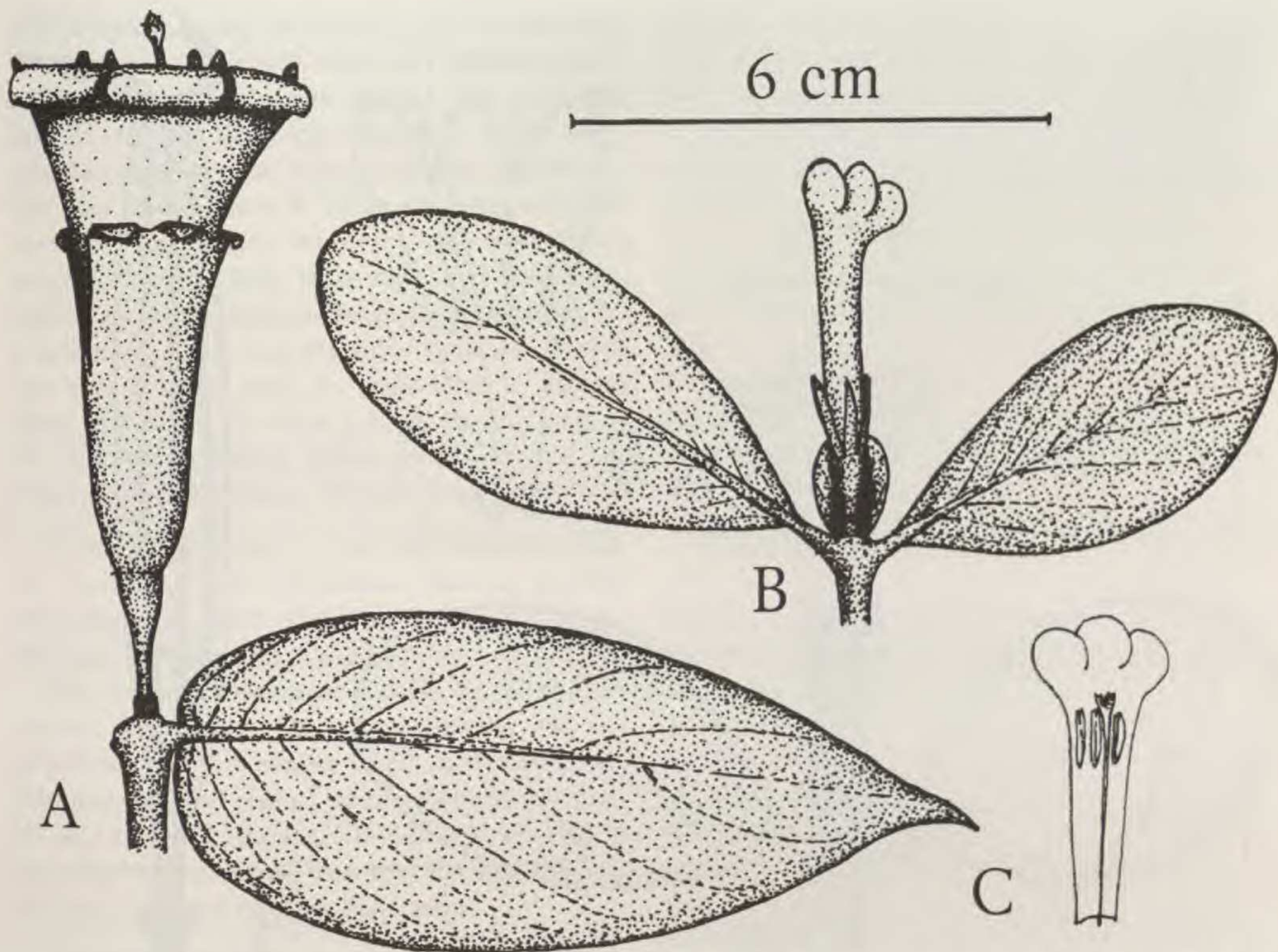


FIGURE 19. A. *Hillia costanensis* Steyermark. —A. Habit with flower. B, C. *Hillia saldanhae* K. Schum. —B. Habit with flower. —C. Flower opened. A, from *Bunting* 14483 (NY); B, C, from *Glaziou* 12790 (F). All to same scale.

in most species of *Hillia*, and the difference in number seen here alone does not seem to warrant separation of these species.

Steyermark separated *H. schultesii* based on its larger leaf blades, 8–11.5 cm long in contrast to 3.5–7 cm long in *H. ulei*, and its “acutish” calyx lobes in contrast to “rounded or obtuse” in *H. ulei*. Based on these distinctions, *H. schultesii* is represented by one collection. Its leaf blades are relatively long, but the “acutish” shape of its calyx lobes is very difficult to separate from the characteristically obtusely angled lobes of *H. ulei*. Given the relatively small number of collections of *H. ulei* available compared to its apparently large geographic range, separation of *H. schultesii* based only on these features seems unjustified.

*Representative specimens examined.* BOLIVIA. **La Paz:** provincia Yungas Sur, basin of Río Bopi, San Bartolomé near Calisaya, *Krukoff* 10171 (A, F, MO). BRAZIL. **Acre:** Cruzeiro do Sul, Rio Jurua and Rio Moa, Estrada Alemanha, *Maas* P12811 (NY). ECUADOR. **Napo:** Río Lagarto Cocha, near Redondo Cocha, 0°35'S, 75°15'W, *Lawesson et al.* 44421 (AAU). PANAMA. **Darién:** Sumacate along Tuyra River, *Pittier* 6594 (US).

PERU. **Loreto:** Mishuyacu near Iquitos, *Klug* 1182 (F, NY, US). **Madre de Dios:** Parque Nacional de Manú, Rio Manú, Cocha Cashu Station, 11°50'S, 71°25'W, *Foster* 9667 (MO, NY). **San Martín:** provincia Mariscal Cáceres, distrito Tocache Nuevo, quebrada de Almendras, margen derecha del río Huallaga, *Schunke* 4458 (COL, F, GH, MO, NY, US). SURINAM. **Nickerie:** lower slopes of Frederik Top, 3 km S of Juliana Top, Wilhelmina Gebergte, 3°36–41'N, 56°30–34'W, *Irwin et al.* 54944 (F).

**17. *Hillia saldanhae* K. Schumann in Mart., Fl. Bras. 6(6): 201. 1889.** TYPE: Brazil. Rio de Janeiro: Nova Friburgo, *A. Glaziou* 12790 (holotype, B destroyed, photos F, GH, MO, NY; isotypes, F, P not seen).

Shrubs; bark red-brown, smooth. Leaf blades elliptic to oblanceolate, 3–6.6 cm long, 1.4–3.2 cm wide, obtuse to rounded at apex, cuneate to acute at base, subcoriaceous; secondary veins pinnate, 7–8 pairs, plane, without domatia; margins flat; petioles 2–7(–10) mm long; stipules 12–15 mm long, 8–10 mm wide. Flowers solitary(–3); peduncles 1–2 mm long; bracts not seen; pedicels

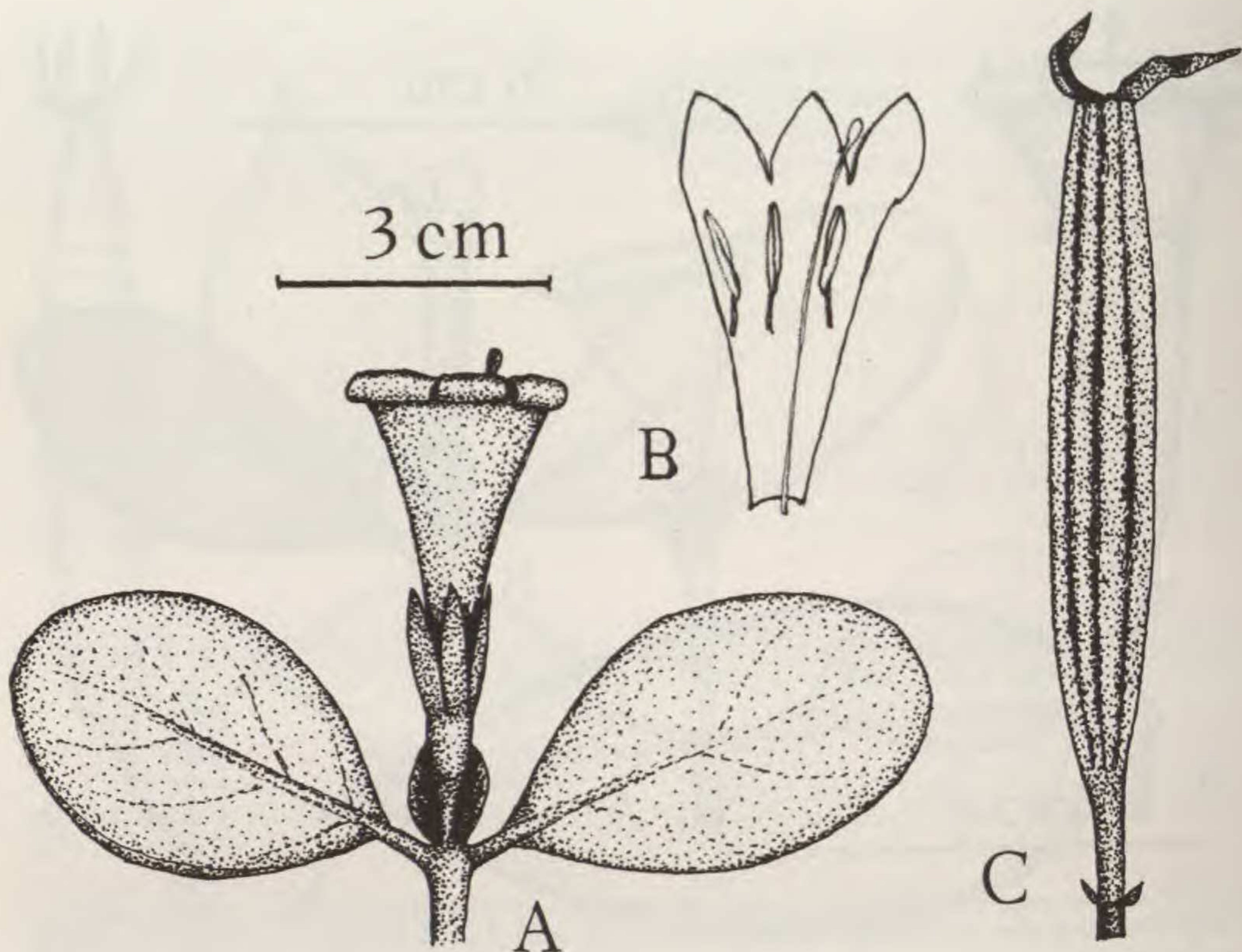


FIGURE 20. A-C. *Hillia foldatsii* Steyermark.—A. Habit with flower.—B. Flower opened.—C. Capsule. A, B, C, from Holst 3772 (MO). All to same scale.

5–10 mm long; calyx limb divided to base, the lobes 5, 9–14 mm long, triangular, acute; corollas narrowly funnellform, the tube 30–35 mm long, the lobes 5, 5–7 mm long, suborbicular, rounded; anthers 5, subsessile, ca. 7 mm long, with tips positioned ca. 6 mm below top of corolla tube; ovary 2–5 mm long; stigmas 1.5–2 mm long, subcapitate, positioned immediately above anthers. Capsules ca. 25 cm long including beak 1–5 mm long, ca. 6 mm diam., not stipitate, smooth or with ca. 8 longitudinal ridges; seeds with filaments ca. 1 cm long. Figure 19A–C.

*Habitat, phenology, and distribution* (Fig. 6). Southeastern Brazil, in wet forest at ca. 100 m. Collection month unknown.

This name has been placed in synonymy with *Hillia parasitica*, but *H. saldanhae* clearly differs from *H. parasitica* in its rounded rather than acuminate leaf blades, five-lobed corollas and calyces, funnellform corollas with short lobes, and anthers positioned near the middle of the corolla tube. It differs from other species of subgenus

*Illustres* by five-merous rather than six- to nine-merous corollas and anthers positioned near the middle rather than the top of the corolla tube. *Hillia saldanhae* resembles *H. foldatsii*; the distinctions between them are discussed in the treatment of the latter species. The corollas of the type collection, measured here, appear to be immature.

**18. *Hillia foldatsii*** Steyermark, Mem. New York Bot. Gard. 23: 290. 1972. TYPE: Venezuela. Bolívar: distrito Piar, Auyantepuí, Valle Orquídeas, parte noroeste, alrededores caída de agua Salto Angel, 1200 m, 17 Aug. 1968, E. Foldats 7192 (holotype, VEN).

Shrubs ca. 1 m tall; bark red-brown, smooth. Leaf blades elliptic, 3–6.4 cm long, 1.5–3.5 cm wide, obtuse to rounded at apex, cuneate to rounded at base, thickly coriaceous; secondary veins pinnate, 2–5 pairs, plane or sometimes with midrib prominulous abaxially, without domatia; margins flat; petioles 3–6 mm long; stipules 9–12 mm long, ca. 8 mm wide. Flowers solitary, with peduncles 4–9 mm long; bracts 2–4.5 × 1–2.5 mm; calyx

limb divided to base, the lobes 6, 13–17 mm long, 3–6 mm wide, narrowly elliptic to ligulate, acute; corollas funnellform, green flushed with pink, the tube 35–60 mm long, the lobes 6, 7–9 mm long, suborbicular, rounded; stamens 6, the filaments 3 mm long, the anthers 9–10.5 mm long, with tips positioned ca. 3 mm below top of corolla tube; ovary 5–10 mm long with stipe 2–3 mm long; stigmas ca. 1 mm long, subcapitate, positioned 4–5 mm above top of corolla tube. Capsules 65–92 mm long including beak 1–5 mm long, 9–12 mm diam., the stipes 10–14 mm long, smooth or with ca. 10 low longitudinal ridges; seeds 2.5–3 × ca. 1 mm, with filaments ca. 12 mm long. Figure 20.

*Habitat, phenology, and distribution* (Fig. 8). Auyantepuí in southeastern Venezuela on rocks in wet forest at 1200–1800 m. Collected in flower and fruit in March and August.

This species is distinguished by its thickly coriaceous leaf blades, six-merous flowers, and exerted stigmas. It is similar to *H. saldanhae*, with subcoriaceous leaf blades, smaller five-merous flowers, and included stigmas. Steyermark reported in the original description that the filaments are 15 mm long, but this has not been seen.

*Additional specimens examined.* VENEZUELA. **Bolívar:** distrito Piar, summit of Auyantepuí, 5°51'N, 62°32'W, *Holst* 3772 (MO).

**19. *Hillia costanensis*** Steyermark, Mem. New York Bot. Gard. 23: 293. 1972. TYPE: Venezuela. Falcón: Sierra de San Luis, cerca del puente de Jobo, entre Curimagua y San Luis, 800–900 m, 20 July 1967, *J. A. Steyermark* 99274 (holotype, VEN; isotypes, NY, P).

*Hillia zuliaensis* Steyermark, Ann. Missouri Bot. Gard. 71: 1176. 1985. TYPE: Venezuela. Zulia: distrito Mara, vicinity of Río Guasare between Rancho 505 and Cerro Yolanda, 10°53–56'N, 72°26–28'W, 200–270 m, 29 May 1980, *J. A. Steyermark* 122876 (holotype, MO).

Suffrutescent herbs or shrubs to ca. 1 m tall; bark gray-brown, smooth. Leaf blades elliptic-oblong to ovate-oblong, 6–13 cm long, 2.3–6.5 cm wide, acute to usually acuminate at apex with tip 5–10(–15) mm long, rounded to slightly cordate at base, coriaceous; secondary veins pinnate, 4–8 pairs, plane or with midrib sometimes prominulous abaxially, without domatia; margins flat; petioles 1.5–3 mm long; stipules ca. 15 mm long, ca. 6 mm wide. Flowers solitary; peduncles 1–3 mm long; bracts lacking or ca. 1 mm long and wide; calyx limb with tube 33–56 mm long, sometimes

splitting along one side, the lobes 6, 3–12 mm long, often unequal by 100%, obtuse; corollas funnellform, bright green to yellow-green, the tube 51–70 mm long, the lobes 6, 8–10 mm long, rounded; anthers 6, subsessile, 10.5–14 mm long, with tips positioned 1–3 mm above top of corolla tube; ovary 5–8 mm long with stipe 5–8 mm long; stigmas ca. 1.5 mm long, subcapitate, positioned immediately above anthers. Capsules 40–61 mm long including beak 1–5 mm long, 5–8 mm diam., stipes 4–8 mm long, smooth with ca. 10 longitudinal lines or low ridges; seeds ca. 3 × 1 mm, with filaments 8–10 mm long. Figure 19A; Steyermark (1974: fig. 23).

*Habitat, phenology, and distribution* (Fig. 8). North-central Venezuela to northeastern Colombia, in wet forests at 200–1300 m. Collected in flower March to May and July, in fruit March, June, and September.

This species is distinguished by its subsessile leaves with the blades rounded to slightly cordate at base and calyx limb with a well-developed tube. Both of these features are unique in *Hillia*. Steyermark distinguished *H. costanensis* and *H. zuliaensis* based on size differences of both vegetative and reproductive features and disjunct geographic ranges. However, with more material available the variation in size and the geographic range seems to be continuous.

*Representative specimens examined.* COLOMBIA. **Guajira:** serranía de la Macuira, cerro Kichuao, cerca del cerro Kalal, *Bernal & Sugden* 85 (COL). **Magdalena:** municipio Santa Marta, Parque Nacional Natural Tayrona, cerro El Cielo, *Lorenzo & Barrera* 3911 (COL). VENEZUELA. **Aragua:** distrito Girardot, Parque Nacional Henri Pittier, La Cumbre de Rancho Grande, 10°21'N, 67°39'W, *Davidse et al.* 16723 (MO, NY). **Lara:** distrito Torres, Páramo Agua Linda, en la carretera Lara–Zulia ca. 35 km al E de El Venado, km 12–13, arriba de la aldea Palmarito, 10°10'N, 70°42'W, *Bunting & Fucci* 13483 (NY). **Portuguesa:** 30 km W of Guanare by air along Río Tucupido, 9°02'N, 70°01'W, *Liesner et al.* 12630 (MO). **Zulia:** Cerro Los Manantiales, E of Río Guasare, W of Hacienda Los Manantiales, 12 km W of Corpo Zulia Campamento Carichuano, 11°01'N, 72°20'W, *Steyermark et al.* 123255 (MO).

**5. *Hillia* subg. *Ravnia*** (Oersted) C. M. Taylor, Selbyana 11: 30. 1989. *Ravnia* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 49. 1853. TYPE: *Ravnia triflora* Oerst. [= *Hillia triflora* (Oerst.) C. M. Taylor].

Five species, southern Mexico to Venezuela. Taylor (1989) described this subgenus and later added two new species (Taylor, 1991), with no

change in its characterization except an expansion of the geographic range. The individual species are therefore not described or discussed here. The geographic range presented for *Hillia triflora* var. *triflora* by Taylor (1989) should be emended to exclude the record from southern Mexico; this was based on a misidentification of a fruiting specimen of *H. loranthoides*. Species placed in this subgenus are *H. allenii* Steyer., *H. longifilamentosa* (Steyer.) C. M. Taylor, *H. oaxacana* C. M. Taylor, *H. rivalis* C. M. Taylor, and *H. triflora* (Oerst.) C. M. Taylor.

## EXCLUDED SPECIES

- Hillia chiriquiensis* Dwyer, Ann. Missouri Bot. Gard. 67: 216. 1980. = *Cosmibuena valerii* (Standl.) C. M. Taylor (Taylor, 1992).
- Hillia liguliflora* Dwyer, Ann. Missouri Bot. Gard. 67: 216. 1980. = *Cosmibuena valerii* (Standl.) C. M. Taylor (Taylor, 1992).
- Hillia longiflora* Blanco, Fl. Filip. 235. 1837, not *Hillia longiflora* Sw. = *Elytranthe ampullacea* (Roxb.) Engl. (Merrill, 1918).
- Hillia longiflora* Hort ex Lem., in Van Houtte, Fl. Serres 3(1): 188. 1847, not *Hillia longiflora* Sw. = *Fagraea zeylanica* Thunb., Loganiaceae.
- Hillia prasiantha* Lem., in Van Houtte, Fl. Serres 3(1): 188. 1847. = *Fagraea zeylanica* Thunb., Loganiaceae.
- Hillia valerii* Standl., J. Wash. Acad. Sci. 16: 164. 1928. = *Cosmibuena valerii* (Standl.) C. M. Taylor (Taylor, 1992).

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NUMERICAL LIST OF SPECIES OF *HILLIA*

1. *Hillia* subg. *Hillia*
  1. *H. wurdackii* Steyerem.
  2. *H. macrophylla* Standl.
  3. *H. macromeris* Standl.
  4. *H. bonoi* Steyerem.
  5. *H. killipii* Standl.
  6. *H. parasitica* Jacq.
2. *Hillia* subg. *Andinae* C. M. Taylor
  7. *H. macbridei* Standl.
3. *Hillia* subg. *Tetrandrae* C. M. Taylor
  8. *H. loranthoides* Standl.
  9. *H. tetrandra* Sw.
  10. *H. maxonii* Standl.
  11. *H. palmana* Standl.
  12. *H. panamensis* Standl.
4. *Hillia* subg. *Illustres* C. M. Taylor
  13. *H. grayumii* C. M. Taylor
  14. *H. psammophila* Steyerem.
  15. *H. illustris* (Vell.) K. Schum.
  16. *H. ulei* K. Krause
  17. *H. saldanhae* Schum.
  18. *H. foldatsii* Steyerem.
  19. *H. costanensis* Steyerem.
5. *Hillia* subg. *Ravnina* (Oerst.) C. M. Taylor
  20. *H. oaxacana* C. M. Taylor
  21. *H. allenii* Steyerem.
  22. *H. longifilamentosa* (Steyerem.) C. M. Taylor
  23. *H. rivalis* C. M. Taylor
  - 24a. *H. triflora* Oerst. var. *triflora*
  - 24b. *H. triflora* var. *pittieri* (Standl.) C. M. Taylor

NUMBERED COLLECTIONS OF *HILLIA* EXAMINED

Specimens are listed alphabetically by principal collector. Identifications are indicated by the numbers in parentheses following the collection number. The numbers in parentheses correspond to the numbers designating the species in the text. Asterisks indicate type collections. All collections cited in the text are included here, along with additional collections of all species not cited in the text.

- Abbott, W. L. 365 (9); 2357 (6). Acevedo, P. 2990 (6). Ackerman, J. D. 1537 (6). Adams, C. D. 11717 (9). Alain, Bro. 3856 (9); 6034 (9). Allen, P. H. 1872 (10); 3682 (10). Alvarez, H. J. 24 (6). Anderson, W. R. 3311 (9); 35844 (6); 35914 (6). Antonio, T. 5078 (10). Ar-

- isteguieta 4239 (6). Arnoldo, Fr. M. 3302 (6). Asanza, E. 41098 (15); 41192 (15). Asplund, E. 10160 (2); 19403 (2); 19458 (3); 19481 (5). Axelrod, F. 240 (6). Barbosa, C. 1906 (6). Barbour, P. 2614 (6). Beaman, J. H. 5185 (9); 6071 (9); 6105 (9); 6475 (9). Belanger 132 (6); 395 (6); 540 (6). Bello, E. 844 (8). Bena, P. 460 (6); 461 (6); 1110 (6); 1163 (6); 1225 (6). Benavides, O. de 9602 (2). Benítez de Rojas, C. D. 1069 (19). Berlin, B. 429 (3). Bernal, H. 48 (19); 85 (19). Berry, P. 3468 (6). Billiet, F. 1916 (15). Blackmore, S. 4104 (9). Blomquist, H. L. 13217 (6). Boldingh, I. 2198B (6). Boom, B. M. 1141 (6); 6901 (6); 6933 (6). Bono, J. 3797 (4). Boudet Fernandes, H. Q. 1830 (6); 2280 (6). Brade, A. C. 6830 (6). Brandebyege, J. 30601 (15); 33903 (15); 33962 (16); 42671 (15). Bresolin, A. 808 (6); 1037 (6). Breedlove, D. E. 31213 (8); 35025 (9); 35244 (9); 48354 (9); 49178 (9); 53555 (12); 56648 (12); 57488 (8); 68610 (8). Brenes, A. 3839 (8); 3847 (8); 3900 (8); 4852 (8); 5439 (8); 6137 (8); 11900 (10); 12644 (11); 15653 (11); 18919 (8). Britton 219 (6); 557 (9); 697 (6); 741 (9); 924 (6); 2020 (6); 2203 (6); 2591 (6); 3377 (6); 3511 (9); 5525 (6); 6378 (6); 5007 (9); 6541 (6); 7561 (6). Broadway, W. E. 5709 (6); 7807\* (15). Brooke, W. M. A. 6700 (6). Bucher, G. C. 47 (9). Buchtien, O. 2217 (6); 5636 (6). Bunting, G. S. 13483 (19). Burch, D. 1371 (6). Byer, M. D. 66-383 (6). Calzada, J. I. 604 (9). Camp, W. H. E2405 (5). Cárdenas 5995 (6). Cardona, F. 207 (6). Carrasquillo 40 (6). Cedillo T., R. 1887 (9); 2757 (9). Chacón, A. 18 (11). Chazaro B., M. 448 (9); 3380 (9). Christ 2188 (6). Churchill, H. W. 5521 (11). Clemente, Bro. 2321 (9); 6626 (9); 7144 (9). Contreras, E. 3024 (9); 5370 (9); 6959 (9); 7911 (9); 8873 (9); 8893 (9). Core, E. L. 1327 (6). Cosentino, K. 21 (9). Correa, M. D. 941 (10); 1770 (12); 2559 (11). Crankshaw, W. 4 (9). Croat, T. B. 14801 (10); 20709 (15); 21093 (6); 23079 (10); 26957 (12); 60971 (6); 63462 (8). Cuatrecasas, J. 12398 (2); 16017 (10); 19988 (10); 23963 (2). Cufodontis, G. 465 (11). D'Arcy, W. G. 1812 (6). Davidse, G. 16723 (19); 20416 (9); 20716 (6); 24028 (11); 25503 (11). Dávila, E. N. 2 (6); 8 (6). de Jesús J., J. 3459 (6). Devia, W. 2572 (2). Díaz, C. 602 (16); 2491 (15). Díaz, S. 2302 (6); 4184 (6). Dickson, J. D. 1352 (9). Dodson, C. H. 1875 (6); 7783 (2); 9136 (2); 10195 (2); 10285 (6); 11852 (6). Donselaar, J. van 2109 (15). Dorantes, B. 3465 (9). Dressler, R. L. 1487 (12); 3522 (11). Drew, W. B. E-553 (2). Dryer, V. J. 1512 (11); 1597 (11). Duarte, A. P. 6257 (6); 11481 (6); 11570 (6). Dudley, T. R. 10414 (6); 11426 (15). Dusén, P. 8109 (6); 8689 (6); 8881 (6); 15538 (6); 15539 (15); 16113 (6). Duss, Père 342 (6); 1462 (6); 2546 (6). Dwyer, J. D. 7377 (10); 10022 (9); 10797 (9). Edwards, J. B. 654 (9). Eggers, B. 6754\* (6). Egler, W. A. 46683 (16). Ekman, E. L. 3775 (6); 4405 (6); 7867 (9); 9989 (9); 15099 (9). Encarnación, F. 26178 (15). Ernst, W. R. 1012 (6). Evans, L. 167 (6). Eyerdam, W. J. 393 (6). Ferreyra, R. 1666 (6); 2255 (8). Folsom, J. P. 4785 (12); 9807 (11). Forero, E. 2868 (15). Fosberg, F. R. 51339 (6). Foster, R. 9667 (16). Galarza, M. 110 (6). Galeano, G. 204 (2). Garnier, H. A. 135 (10). Gaudichaud 625 (6). Gentle, P. H. 3006 (9); 4847 (9); 4930 (9); 8939 (9). Gentry, A. 24168 (2); 35166 (2); 40719 (10); 45322 (6); 50447 (6); 50701 (6); 50959 (6); 50959A (9); 52091 (6); 59053 (15);

60342 (2); 60442 (2); 72567 (6); 77121 (9). Ginzberger, A. 273 (6). Glaziou, A. 6588 (6); 12790A (15); 13943 (6). Gómez G., L. D. 23593 (8). Gómez L., J. 11095 (11); 11302 (11). Gómez P., A. 4525 (9); 5447 (9). Gounelle 63 (6). Granville, J. J. de 4362 (15); 5856 (6); 6146 (15); 6215 (6); 6519 (15); 6797 (15); 8563 (6). Grayum, M. 2793 (13).

Haber, W. 384 (12); 562 (12); 571 (10); 760 (11); 1156 (11); 1342 (11); 1787 (8); 3671 (11); 3672 (12); 4263 (11); 4267 (11); 4501 (8); 4530 (11); 4564 (11); 5273 (12); 5275 (10); 6174 (11); 7000 (8); 7083 (11); 7334 (11); 8370 (8); 8393 (8); 8464 (13); 8914 (11). Hahn, L. 959 (6). Hallé, F. 591 (15); 622 (15); 698 (6). Hammel, B. E. 1284 (11); 2212 (11); 13930 (11); 13933 (10); 17336 (13). Hamilton, C. 4042 (10). Harley, R. M. 19309 (6); 19684 (6); 20860 (6); 27773 (6). Harling, G. 3884 (6); 11639 (6); 12475 (6); 24490 (3). Harris, W. 5465 (9); 9448 (9). Hartley, T. G. 13342 (6). Harvard Tropical Botany Course 797 (9). Hatheway, W. H. 1371\* (11). Hatschbach, G. 7172 (6); 14528 (6); 18509 (6); 20831 (15); 23346 (6); 25789 (6); 28833 (6); 29669 (15); 39314 (6); 40653 (6); 43257 (6); 46043 (6). Hayden, Sr. M. V. 1021 (12). Heller, A. A. 4612 (6). Henrich, J. E. 406 (11). Hernández G., H. 124 (9); 1244 (9). Hernández M., R. 1256 (9); 1374 (9). Herrera Ch., G. 438 (10); 564 (8); 674 (11); 1320 (2); 3910 (10). Hesperheide, H. A. 519 (6); 541 (6); 986 (9); 1389 (9). Hioram, Bro. 4259 (9). Hodge, W. T. 702 (6); 1802 (6); 1663 (6); 1839 (6); 2587 (6); 3110 (6). Hoehne, F. C. 11504 (6). Holm-Nielsen, L. 4202 (15); 6124 (6). Holst, B. K. 3772 (18); 4292 (12). Hoover, W. S. 1920 (3). Howard, R. A. 10587 (6); 11515 (6); 11832 (6); 11954 (6); 12277 (6); 13436 (9); 14290 (9); 15540 (6); 16052 (6); 16053 (6); 16634 (6); 16889 (6); 17553 (6); 17675 (6); 19404 (6). Houghton, W. M. 1194 (6). Huber, O. 6316 (6); 8085 (6). Hunt, D. R. 6473 (6). Hutchison, P. C. 6799\* (1).

Ibarra M., G. 202 (9); 547 (9); 1025 (9); 1983 (9); 1984 (9). Idrobo, J. M. 1059 (2); 2356 (6). Iltis, H. H. G202 (8). INBio-I 181 (11). Irwin, H. S. 19852 (6); 30209 (6); 54944 (16); 55298 (15); 55870 (15).

Jack, J. G. 6812 (9); 7211 (9); 8572 (9). Jacobs, B. 2265 (13). Jameson, W. 532 (6). Jaramillo A., J. L. 56 (5); 6897 (15). Jaramillo M., R. 7072 (6); 2748A (2). Játiva, C. 285 (2). Jean-Pierre, L. L. 238 (6). Jelski, C. de 367 (6). Jérémie, J. 832 (6); 1040 (6); 1099 (6); 1284 (6). Jiménez M., A. 2075 (11). Johnston, J. R. 41 (6); 1563 (6). Jorgensen, O. H. 40 (6). Jousson, J. 624A (6). Judd, W. S. 1508 (6).

Kennedy, H. 578 (11). Killip, E. P. 20685\* (5); 34972\* (10); 38670 (10). Kirkbride, J. H., Jr. 858 (10); 2398 (6). Klein, R. M. 7889 (6); 10641 (6); 10758 (6). Klug, G. 1182 (16); 3145 (5). Knapp, S. 2159 (10); 2621 (10); 4161 (11); 4205 (10); 4953 (11); 5398 (11); 7492 (1). Krukoff, B. A. 10171 (16); 10697 (15). Kuhlmann, G. G. 15737\* (16). Kuhlmann, M. 1750 (6). Kuntze, O. 486 (6).

Landrum, L. R. 4273 (6). Lanjouw, J. 628 (15). Lankester, C. H. 1935 (11). Lanna 1922/1463 (6). Lawesson, J. E. 44288 (15); 44317 (15); 44421 (16). Lawrance, A. E. 351 (6). Lawton, R. O. 1254 (11). Lehman BT 416\* (3). Lemos, C. 28681 (6). Lent, R. W. 1692 (8); 3703 (13). León, Bro. 6626 (9); 7854 (9); 19805 (9). León, J. 2999 (12). Lewis, M. 40471 (16). Liebmman 15419 (9). Liesner, R. 8170 (6); 8423 (6); 12360 (19); 12775 (6); 18431 (6). Lindeman, J. C. 13462 (6). Linden 786 (6); 2169 (6). Liogier, A. H.

11207 (6); 14372 (6); 17484 (6); 17770 (9); 18421 (9); 20366 (6); 21526 (6). Little, E. L., Jr. 8876 (6); 13094 (6). Lloyd, F. E. 164 (6). López F., M. 1637 (9). Lozano C., G. 2972 (6); 3774 (6); 3911 (19); 4967 (2); 5449 (2). Lugo S., H. 1749 (2). Luna, A. 48 (9). Lundell, C. L. 6232 (9); 6372 (9); 6799 (9); 16300A (9); 18226 (9). Luteyn, J. L. 3335 (11); 8738 (2); 11542 (6); 12690 (10); 12698 (6).

Maas, P. J. M. 12811 (16). Macbride, J. F. 5760\* (7). MacDougal, J. M. 3719 (2). MacDougall, T. 5658 (9). Madison, M. T. 4519 (2); 4700 (10). Maguire, B. 24009 (15); 28522 (6); 35287\* (6); 35296 (6). Makrinus, E. 727 (8). Marcano B. 70-2-77 (15). March 1490 (9). Marín 2192 (6). Martens, P. 7076 (6). Martinelli, G. 9593 (6). Martínez S., E. M. 7969 (9); 15074 (9); 15574 (9); 15589 (9); 16660 (9); 18806 (9); 22911 (9); 22922 (12); 22953 (12). Martínez C., G. 3075 (9). Matuda, E. 17722 (9). Maxon, W. R. 2958 (9); 7501\* (10); 8045\* (10). McDaniel, S. 14422 (9); 25763 (16). McPherson, G. 6858 (10); 7138 (10); 8328 (11); 8941 (10); 10577 (11); 11846 (10); 13407 (6); 13449 (6). Meclinors 35 (15). Mejía, M. 299 (6); 4995 (6); 23929 (9); 35780 (9); 35781 (6). Mello B. 3605 (6); 5091 (6). Menéndez L., F. 85 (9). Miers, J. 4023 (6). Miller, J. S. 5999 (6). Molina, A. 17169 (12); 17259 (10). Morales, G. 528 (6). Moreira, C. 53 (6). Moreno, P. P. 8510 (11); 16513 (11); 18806 (12); 19112 (9); 19689 (12); 19852 (12); 23735 (9); 24904 (11); 24936 (11). Mori, S. 4873 (11); 5815 (10); 5947 (10); 6095 (11); 6500 (10); 7559 (11); 13292 (6). Morley, B. D. 917 (9). Morton, C. V. 3219 (9). Moya, S. 106 (6). Mutis, J. C. 3655 (2).

Nash, G. V. 1753 (6). Nee, M. 18764 (9); 22719 (9); 24986 (9). Neill, D. 382 (11); 1924 (9); 7259 (9).

Oldeman 38 (6). Orozco, J. M. 142 (11). Otero, J. I. 639 (6). Ownbey, M. 2669 (2); 2737 (5).

Palacios, W. 4433 (15); 6540 (5). Pennell, F. W. 5890 (2); 5898 (6). Pinto E., P. 6233A (15). Pittier, J. 3190\* (12); 6594 (16). Plowman, T. 2862 (6); 13370 (6). Pounds, W. Z. 221 (11). Poveda, L. J. 1664 (11). Prance, G. T. 9436 (6); 29385 (6). Primack, R. 363 (11); 403 (11). Proctor, G. R. 16999 (6); 17634 (6); 22567 (9); 32634 (9). Purpus, C. A. 262\* (12).

Quentin, R. P. 488 (6). Questel, A. 1628 (6); 2257 (6); 4756 (6).

Ramiz G. 503 (6). Reitz 1825 (6); 2058 (6); 5789 (6). Reko, B. P. 6 (9). Restrepo 449 (2). Revilla, J. 576 (16); 858 (15). Riedel 1240 (6). Robinson, J. W. L. 200 (2). Robleto, W. 138 (9). Rodríguez, L. 2739 (6); 4454 (6); 4460 (6). Roig, J. T. 6104 (9); 6650 (9). Romero C., R. 6753 (6); 7010 (6); 7027 (6); 7803 (6). Roviroa, J. N. 577 (9). Rusby, H. H. 863 (6).

Sagástegui A., A. 5997 (1). Samp, A. 6896 (6). Sánchez, V., J. G. 317 (1). Sandeman, C. 3672 (5). Sargent, F. H. B155 (6); 590 (6). Sastre, C. 1934 (6). Schipp, W. A. S-585 (9). Schultes, R. E. 13030 (15); 13075\* (16). Schunke, C. A100 (7); 290 (6); 436 (7). Schunke V., J. 4458 (16); 4784 (16); 5247 (6); 5317 (6); 7672 (6); 8170 (6); 8380 (3); 10292 (15); 11391 (6). Seibert, R. J. 495 (10). Seifritz, W. 1038 (9). Sello 1754 (6); 5988\* (15). Shafer, J. A. 3137 (9); 3297 (6); 3443 (6); 3619 (6); 8004 (6); 8551 (9). Silva, N. T. 927 (15). Simpson, D. R. 806 (15). Sintenis, P. 151B (6); 525 (6); 1609 (6). Slane, V. 607 (6). Smith, A. 120 (11); 2737 (12); 2678 (11). Smith, A. C. 10256 (6); 10549 (6). Smith, D. N. 4139 (6); 4385 (5); 6323 (6). Smith, H. H. 725 (6); 1654 (6). Solomon, J. C. 10826 (6); 13957 (15). Spellman, D. 1639 (9). Spruce, R. 5079 (6); 6186\*

- (2). Standley, P. C. 38472 (10); 42187 (10); 42599 (10); 42771 (10); 44733 (10); 44738 (11); 46152\* (8); 50144 (10); 50691 (10); 52736 (9); 54583 (9); 55581 (9); 68706 (9); 84616 (9); 84893 (9); 91610 (12). Steere, W. C. 8070 (6); 8196 (6). Stehlé, H. 187 (6); 334 (6); 429 (6); 868 (6); 4688 (6); 6005 (6); 6060 (6); 7406 (6); 8115 (6). Stein, B. A. 3108 (2); 3564 (6). Steinbach, J. 9026 (6). Stevens, W. D. 5628 (11); 5947 (11); 6552 (12); 7404 (9); 9616 (11); 11558 (11); 11679 (11); 23919 (12); 24389 (12); 24958 (13); 25120 (13). Steyermark, J. A. 381 (6); 1140 (6); 31627 (12); 33183A (9); 33502 (9); 35211 (9); 33667\* (8); 36731 (9); 37255 (9); 39464 (9); 44195 (12); 44435 (9); 46048 (9); 46606 (9); 46808 (9); 47954 (9); 52827 (2); 54093 (6); 55808 (6); 56156 (6); 56591\* (6); 59799 (6); 61433 (15); 62044 (6); 75974 (6); 88052 (15); 88835 (15); 93882 (6); 94089 (6); 94645 (6); 99274\* (19); 99777 (19); 103708 (6); 104445 (6); 106214 (6); 106453 (6); 116874 (6); 122876\* (19); 123255 (19). St. Hilaire B2243 (6). Stimson, W. R. 1870 (6). Sturrock 460 (6). Sugden, A. M. 217 (19); 1026 (6). Sutton 218 (9). Tate, G. H. H. 710 (6). Taylor, C. M. 6353 (6); 10445 (6). Taylor, N. 519 (9). Terborgh, J. 357 (6). Tessene, M. F. 1377 (11). Tessmann, G. 4020 (6). Timaná, M. 823 (5); 827 (5). Ton, A. S. 3853 (8). Tonduz, A. 17755 (10). Tuerckheim, H. von II340 (9); II2254 (9); 7920 (9). Tyson, E. L. 3436 (11). Ule, E. 4422 (6); 6305\* (16); 15737 (16). Uribe U., L. 3197 (2). Utley, J. 2609 (11); 5223 (11). Valdivia Q., P. 766 (9); 951 (9); 1423 (9). Valerio R., J. 1359 (8). Vareschi 4771 (6). Vargas, C. 15615 (6). Vásquez, R. 4116 (3); 4130 (15); 6421 (15); 10091 (15); 11879 (16). Vaught 305 (8). Vauthier, M. 77 (6); 96 (6). Vélez, I. 786 (6). Ventura A., F. 20644 (9). Wadsworth, R. K. 443 (6); 492 (6); 617 (6). Wagner, R. J. 176 (6); 1680 (6); 1752 (6). Webster, G. L. 209 (9); 13239 (6); 15378 (9). Weddell, M. 1520 (6). Wendt, T. 2775 (9); 4451 (9); 5779 (9). Werff, H. van der 6722 (10). Weston, A. S. 10198B (11). Wilbur, R. L. 7389 (6); 7816 (6); 7845 (6); 7947 (6); 16929 (11); 19782 (11); 29803 (11). Williams, Ll. 99 (15). Williams, L. O. 7916 (6); 13068 (9); 15135 (9); 28129 (10); 41950 (8). Williams, R. S. 1478 (6); 11003 (6). Wilson, P. 172 (6). Wingfield, R. 6647 (6). Woytkowski, F. 8236 (1). Wright, C. 125B (6); 266 (9); 1256 (6). Wurdack, J. J. 1027 (1). Zak, V. 3788 (7). Zamora, N. 619 (11). Zanoni, T. 12914 (6); 18867 (6); 19853 (6); 21127 (9); 22508 (6); 24771 (9); 26660 (6); 35437A (6); 35961 (9). Zarucchi, J. L. 1885 (15); 4168 (2); 5659 (6).